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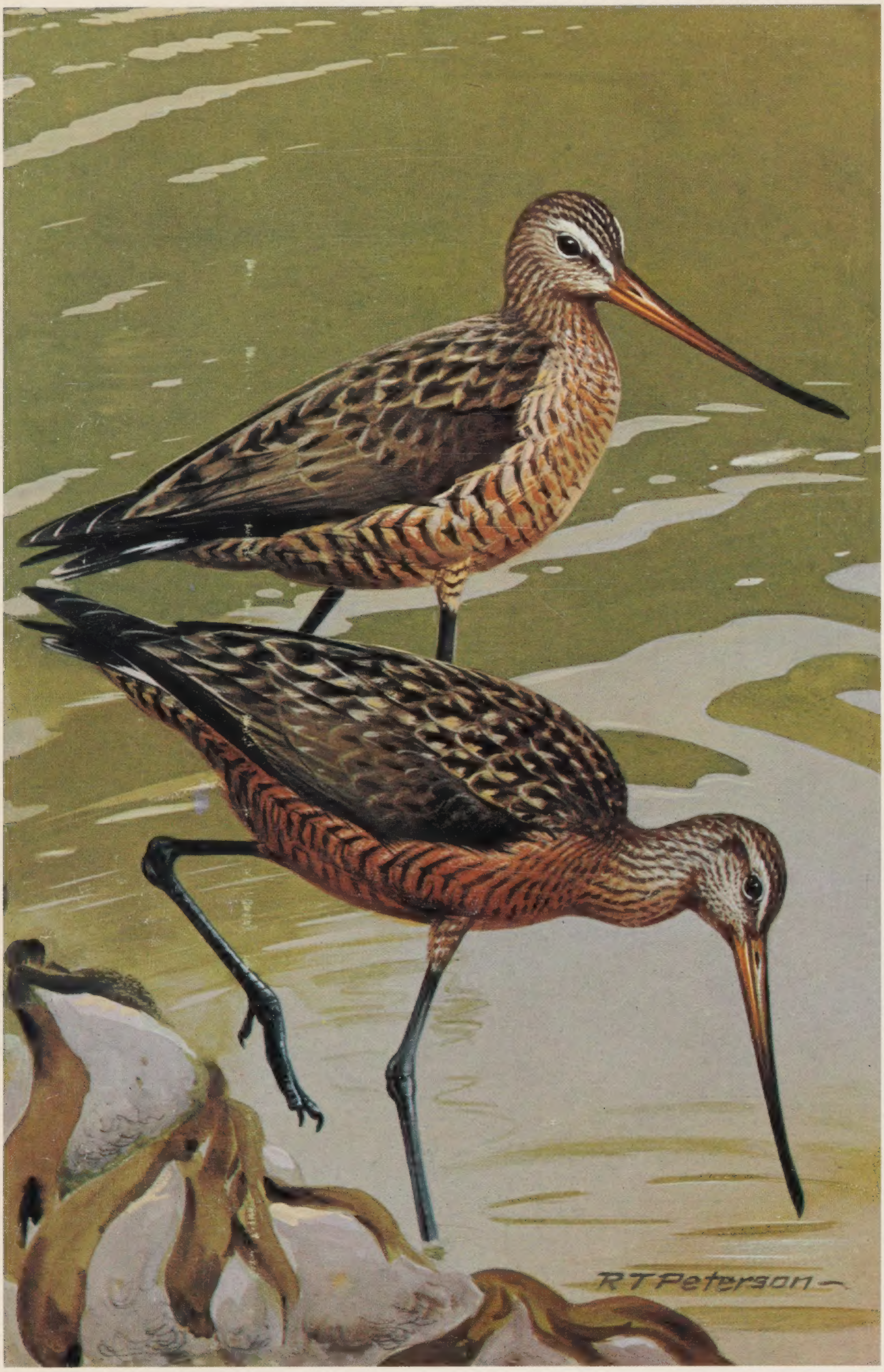
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Cornell Laboratory of Ornithology

THE LIVING BIRD

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Cornell Laboratory of Ornithology

1966

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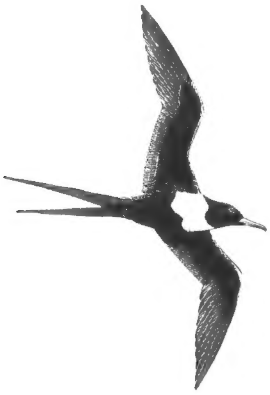

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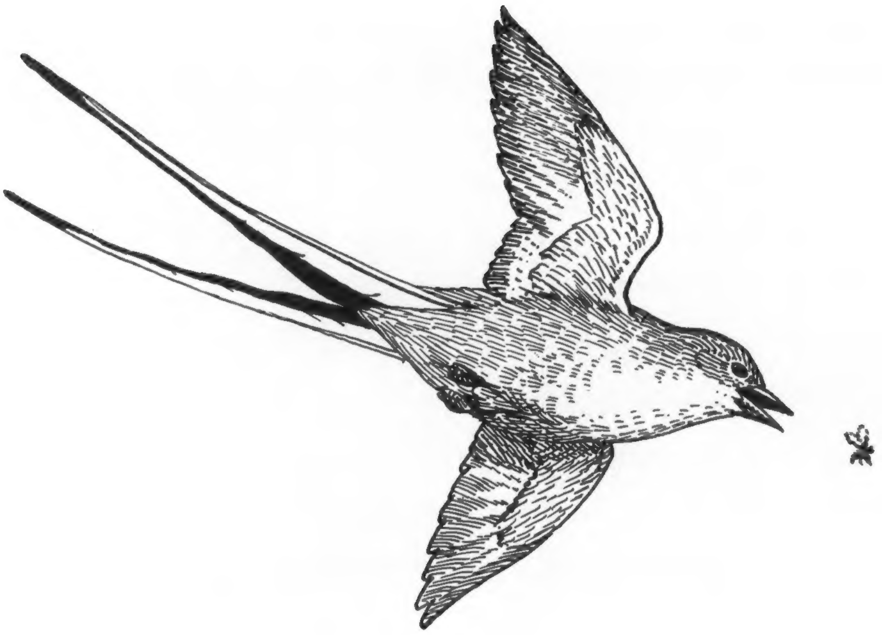

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CONTENTS

NESTING OF THE HUDSONIAN GODWIT AT CHURCHILL, MANITOBA. *Joseph A. Hagar* 5

THE BEHAVIOR AND ECOLOGY OF THE SOUTH AFRICAN OSTRICH. *E. G. Franz Sauer* and *Eleonore M. Sauer* 45

SPECULATIONS ON THE ORIGIN OF FEATHERS. *Kenneth C. Parkes* 77

Note by Illustrator. *Rudolf Freund* 84

THE ACTIVITIES AND COACTIONS OF ANIMALS AT SAPSUCKER TREES. *William L. Foster* and *James Tate, Jr.* 87

THE PECKING RESPONSES OF PEAFOWL CHICKS. *William C. Dilger* and *J. Cherrill Wallen* 115

REGIONAL VARIATION IN THE SONG OF THE CAROLINA CHICKADEE. *Rodman Ward* 127

SOME OBSERVATIONS ON HABITATS OF THE SWAINSON'S WARBLER. *Brooke Meanley* 151

HEARING LOSS AND BIRD SONG. *Harold Mayfield* 167

GROUND-NESTING GREAT HORNED OWL: A PHOTOGRAPHIC STUDY. *Frederick Kent Truslow* 177

THE ROLE OF MIGRANT BIRDS AT SWARMS OF ARMY ANTS. *Edwin O. Willis* 187

AUTHORS AND ARTISTS BRIEFLY NOTED 233

STAFF, ADMINISTRATIVE BOARD, RESEARCH ASSOCIATES, AND FIELD ASSOCIATES OF THE LABORATORY OF ORNITHOLOGY, 1965-1966 . . . 235

MEMBERS OF THE LABORATORY OF ORNITHOLOGY, 1966 237

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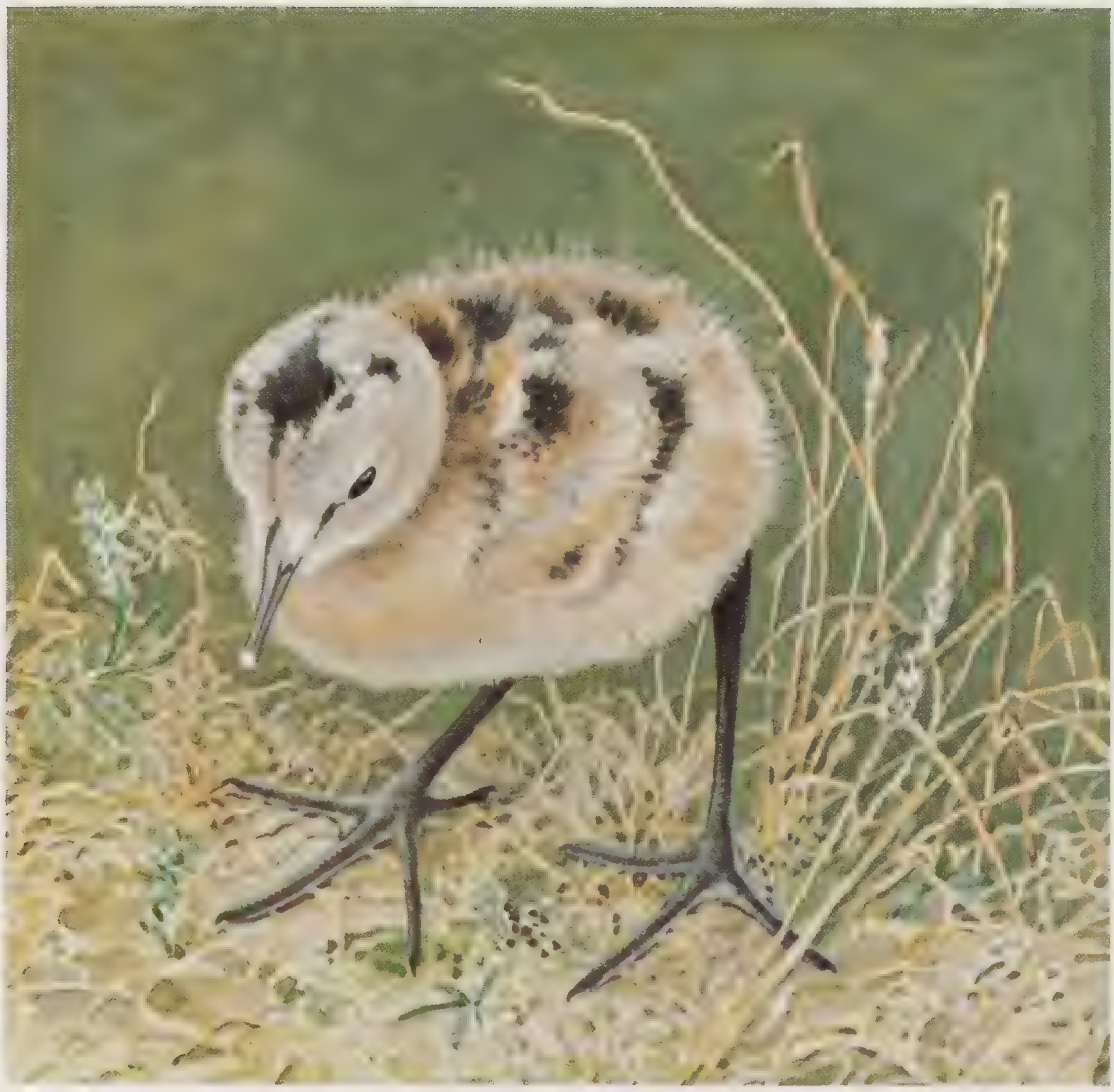


Chick of the Hudsonian Godwit
Painting by George Miksch Sutton.

NESTING OF THE HUDSONIAN GODWIT AT CHURCHILL, MANITOBA

Joseph A. Hagar

Photographs by the author

Since the time of Nuttall and Audubon, 130 years ago, most of the published references to the Hudsonian Godwit (*Limosa haemastica*) have treated it as uncommon, and from the 1930's until about 1960 it was frequently listed as a threatened species, on its way to early extinction. Actually its status is quite different. Thus, before coming to the main subject of this paper, I feel a necessity for reviewing what is now known of its numbers and post-breeding distribution.

Status and Post-breeding Distribution

The Hudsonian Godwit is a common breeding bird within a somewhat specialized but not unduly restricted range in central and northwestern Subarctic Canada; and on the west shores of Hudson Bay and James Bay (Figure 1) it is conspicuous in migration by reason of the very large flocks into which it gathers at the end of summer. It is, to be sure, uncommon in the settled parts of Canada and the United States during its travels to and from a wintering range in southern Argentina and Chile, but this is due to the nature of its migrations, which not only carry it through regions where scientific observation is irregular or entirely wanting, but also appear to involve one or more of the most remarkable long distance non-stop flights among all birds. The requirements of physiological preparation for the fall migration place a strict limit on the length of the nesting cycle and so have a bearing on my subject.

The records which reveal the abundance of the Hudsonian Godwit along its Canadian migration route go back nearly 300 years, to the first arrival of English fur-traders in 1670, but they are so widely spaced in time, so casual in their nature, and, in some cases, so obscurely published that, until recent years, they have not attracted much attention. This situation began to change about 20 years ago when C. E. Hope and T. M. Shortt of the Royal Ontario Museum reported on a 10-day trip by canoe, in July 1942, down the lower west coast of James Bay (Hope and Shortt, 1944). Leaving Fort Albany on 15 July, they camped four days at the mouth of the Nettichi River, four days at Big Piskwanish Point, and arrived at Moosonee on 25 July. Whether by chance or design, they made their trip when the first heavy movement of southbound shorebirds was flooding down the west shore; they saw the main flight of adult Whimbrels, enormous packs of Knots and small sandpipers,

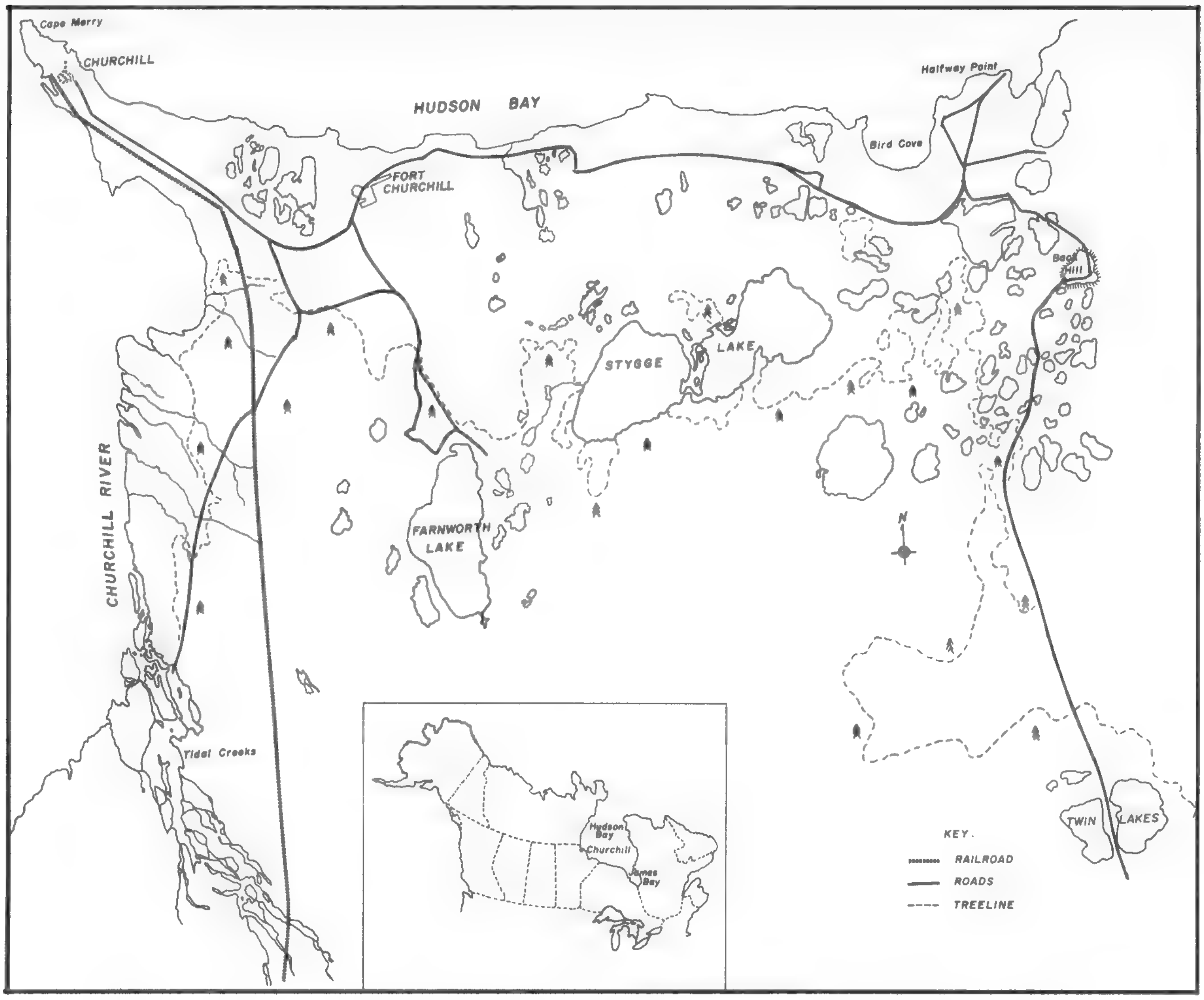

Cape Merry
CHURCHILL
HUDSON BAY
Halfway Point
Bird Cove
FORT CHURCHILL
STYGGE LAKE
Hill
CHURCHILL RIVER
FARNWORTH LAKE
N
Tidal Creeks
Hudson Bay
Churchill
James Bay
TWIN LAKES
KEY.
RAILROAD
ROADS
TREELINE

Figure 1. Map of the Churchill area in Manitoba on the west coast of Hudson Bay.

and, somewhat to their surprise, upwards of 1,200 Hudsonian Godwits. The bulk of these—"at least 1000"—passed the Piskwanish camp in about an hour and a half on 23 July; and on the next day, 200. Most flocks were in the 60 to 70 range; a few ran up to 125; and the 10 specimens collected were all adults in the early stages of molt.

This was more Hudsonian Godwits, by far, than had been noted since the first years of the century, and in due course led to renewed interest in the bird. Working backward through the records, it is evident that these are wholly consistent, however scattered, and the new reports which began to come in from game managers and biologists after 1945 confirmed their validity. I saw parts of the godwit migration on the coast of James Bay in 1955 and 1965, and have had the benefit of either oral information or copies of field notes from eight other reliable observers who were there, on one errand or another, at the appropriate season. This material, in more detail, will be published shortly as a separate paper. Meanwhile the records provide an ample base for the outline of fall distribution which follows.

In the last two weeks of July, from the 17th on, adult Hudsonian Godwits gather on the tidal flats of Hudson Bay and begin to move southeastward. Those individuals which have been guarding chicks are thin, while others, whether subadults or unsuccessful nesters, are already putting on fat; and all continue to do so in long days of industrious feeding. Flocks are small at first, but tend constantly to aggregate. By 23-26 July the vanguard of adults is well down the west coast of James Bay beyond the southern limits of nesting. Within a day or two of 5 August, the first juveniles appear on the flats and soon gather into flocks of their own kind; unlike the adults, they do not begin at once to move southeastward. For a week or 10 days in mid-August, virtually the whole species, old and young, is concentrated in a coastal strip averaging only a few miles in width but stretching a thousand miles in length, from Eskimo Point on the Keewatin shore north of Churchill to the foot of James Bay. At the favored gathering places they are now in packs of many hundreds, with smaller flocks scattered between; most of the adults are already south of Cape Henrietta Maria, the juveniles still north of Akimiski Island. The last two weeks of August see the main departure of adults from the southern end of James Bay. The peak is usually a day or two either way from 23 August, and the number of birds passing a given point on the coast, between midafternoon and dark of a flight-day, sometimes exceeds three or four thousand. The direction of departure is within a few degrees of southeast, and the flocks are relatively large—from 70 to 350. In the meantime the young-of-the-year begin to move southeastward and by 10 September their packs are building up on the same grounds recently vacated by the adults. Although actual data are few, they presumably leave in the same manner, between 15 September and 10 October.

While the total numbers mentioned in the foregoing account will seem quite incredible to anyone who still thinks of the Hudsonian Godwit as rare, the key fact is the size of the flocks, for with a single exception there seem to be no published records of such flocks as these at any point between James Bay and the southern half of South America. From Barbados, in the Lesser Antilles, there is one old reference which reads, ". . . on the 10th of October, 1878 [i.e., at the season of juvenile migration] this species passed over the island in large and continuous flocks the whole day . . ." (Feilden, 1889). Other evidence than this is almost lacking. Along the upper Atlantic coast very few records, either old or recent, are for more than 100 godwits in a flock at one place and time. South of New Jersey on the coast and in any other part of the United States, 10 birds together in the fall are unusual. For all of the West Indies except Barbados, the largest flock reported is 30 in the Dominican Republic (Wetmore, 1931). In northern South America the definite records concern only a bird or two, here and there; none of the regional references implies the presence of large flocks or great flights either on the coast or inland. Only from Argentina and Chile, beyond 35° S Lat., is the species reported in numbers which begin to match the James Bay departures, and these data are both old and few.

In attempting to appraise this scarcity of records, I would limit my speculation by assuming that the bird has stopping places, as yet undiscovered, in northern South America. The observed departures from James Bay are on courses which lie between 30 and 40 degrees east of south, and several bits of evidence suggest that this direction is maintained throughout. If so, the flocks go to sea above the southern New England coast, pass to the west of Bermuda, follow down the general line of the eastern Lesser Antilles, and reach the South American coast somewhere between the mouths of the Orinoco and Amazon Rivers. This coast includes great stretches of tidal mud flats and lagoons which are but little known to ornithologists, and certainly under no sort of regular observation. Like several other shorebirds, godwits tend to gather in numbers at some places and to avoid others which are much the same; unless the concentration points are found, the birds may appear to be scarce or altogether absent. These combined circumstances make it possible that a stopping place in South America remains unnoticed, and both physiological necessity and a scattering of October-November arrival dates in Argentina and Chile make it probable. On the other hand, because the Caribbean islands and the Atlantic coast of North America are so well and regularly worked for their birds that large flocks of godwits would certainly have been detected before now, there is only the slightest chance of a normal stopping place north of the Orinoco delta. I draw the conclusion, with only such reservations as attach to all circumstantial evidence, that the passage from James Bay to the South American coast is accomplished without break.

This is, on its face, an extraordinary flight which loses nothing by closer examination. The distance involved in a great circle course to the mouth of the Orinoco is approximately 2,800 miles. Taking into consideration that many flocks begin the flight from points well up the James Bay shore, that some may deviate from a great circle route, and that others may overfly the South American coast before stopping, it seems reasonable to suppose that the average span is beyond 3,000 miles. Very few birds, all of them shorebirds, can be even suspected of a non-stop flight so long as this, and for none is the evidence as good. Of other species, some flocks and individuals unquestionably make extended flights, but their departure points are so scattered and the possible stopping places so many or so little observed that we cannot know which birds have flown far and which have paused on the way. For the Hudsonian Godwit, this doubt is largely resolved: in general terms, the whole species leaves from a relatively small area, and, flying over a course which is well watched for at least 2,800 miles, literally disappears from sight until it arrives on the wintering grounds. The performance of the juvenile birds is particularly impressive. At 10 weeks from the egg they set forth, without adult guidance, on the same migration as the adults and they are already so strong on wing that we have no instance of a sizable flock of them being forced down by bad weather. In this they appear to outstrip even the adults. They never land in numbers on the New England coast in late September and early October, as the latter occasionally do at the end of August. There may be some meteorological explanation, but the fact remains and gains force by comparison with American Golden Plover migration, in which the adults take the long over-water route, while many or most of the juveniles move by shorter overland stages.

Necessarily, so long a flight as this involves certain adaptations of structure, physiology, and habit. The Hudsonian Godwit shows such modifications and, while they do not differ in kind from those of other Arctic-nesting shorebirds, we may expect a high degree of development. The chief adaptation, lying outside the field of this paper, is the capacity for storing fat in anticipation of flight and metabolizing it rapidly during flight. Those adaptations which appear during the reproductive period, though less important, still contribute to the end result—a series of small economies which telescope the breeding cycle into a minimum of time. This compression of the nesting season only acquires its full measure of interest when viewed against the migration so soon to follow.

Scope of Study

Although the history of the Hudsonian Godwit on its nesting grounds goes back a hundred years, its substance is almost wholly recent. Finding of the first nests and eggs between 1862 and 1866, in the Anderson River valley of northwestern Canada, was reported by MacFarlane (1891). At least two sets of eggs were taken by J. O. Stringer in 1897 and 1899, somewhere on the

Mackenzie River delta (see Bent, 1927). Neither collector left more than the briefest description of the circumstances, and no further information came to light until 1930, when the railroad to Churchill (Figure 1), on the Hudson Bay coast of northeastern Manitoba, was nearing completion.

P. A. Taverner and A. C. Lloyd, making the first reconnaissance of the Churchill region in that year, noted a pair of godwits on the site of the new town from 29 May until 4 June when they collected them and found two well-developed eggs in the female. In 1931, a Carnegie Museum party, which included G. M. Sutton and O. S. Pettingill, Jr., worked the region more extensively and turned up the equivalent of perhaps eight or ten pairs. Two pairs on 1 July "behaved as if they had eggs or young . . . . The species probably nests in scattered pairs back in the muskeg country . . ." (Taverner and Sutton, 1934). This news soon spread, and in the next 15 years Churchill was visited by a surprising number of bird-minded people whose interest, though general, was not less for knowing that a godwit's nest could be included on the list of local possibilities. Several experienced egg collectors returned again and again to renew their searches, but with no success. As the 1946 season came to an end, neither eggs nor young birds had yet been discovered.

The reporting of the first nest, if not its actual finding, fell to the lot of Hazel R. Ellis (1948). Dr. Arthur A. Allen had suggested a Churchill trip to Miss Ellis. When she raised the question of an objective, he replied: "Find the nest of the Hudsonian Godwit." For this reason, she was perhaps the most single-minded of all the searchers, with time to exploit the lead which came her way. She arrived on 11 June 1947, and three days later, during a chance encounter with a party of army entomologists working on mosquito control, was told of an unidentified nest which one of the men, W. C. McDuffie, had happened on that morning when he walked out from the road to make some dippings for larvae. He took her back to see it and, as they approached, a Hudsonian Godwit flushed from two eggs. Miss Ellis watched this nest after the clutch was completed and, when three of the eggs hatched on 8 July, she and her companions were the first people on record to set eye on the downy young. A photograph, showing clearly the diagnostic head markings, accompanies her paper. Four years later, Dr. Russell T. Congdon (1952; also, Congdon and Congdon, 1952) found and photographed two godwit chicks on 15 July 1951; and in 1954 Dr. Allen and Dr. Peter Paul Kellogg discovered a second nest with eggs and observed the hatching of chicks on 2 July and recorded the event on tape for the Library of Natural Sounds at the Cornell Laboratory of Ornithology.

The studies upon which this paper is based were made in the five-year period 1961-1965, in somewhat different circumstances than obtained before that time. Most of the earlier work on birds at Churchill was done in the only area which then had trails or roads—a block of country about seven miles long and five miles wide on the east side of the river upstream from the townsite. However, a much larger block lying farther eastward was gradually opened up by the winter trails required for military use, and eventually a graded all-season road was pushed out in that direction. Leslie M. Tuck, Canadian Wildlife Service, was the first ornithologist to take advantage of this road when he studied nesting Common Snipe near its farther end in the season of 1961. He found Hudsonian Godwits common on his area and came across several nests while hunting for snipe nests. Knowing of my interest in the species, he very kindly supplied some notes which called my attention to the opportunities for studying Hudsonian Godwits at Churchill.

My first and longest visit was in 1962 with Thomas H. Foster. We arrived on 31 May, made our headquarters in town through 25 June, camped at points 15 miles southeast and eight miles east of town through 28 July, and left on 31 July. In 1964, I reached Churchill alone on 9 July for further observation of the chick-rearing period and stayed through 30 July. Two other parties had preceded me that year: Joseph J. Jehl and Charles G. Yarbrough in the last week of May and David F. Parmelee with companions in early June. Parmelee left before my arrival; Jehl and Yarbrough were still there on my departure. Jehl returned for further work in 1965, having D. J. T. Hussell with him that season, and remained until the third week of July.

Both Jehl and Parmelee have been generous in providing me with copies of their notes on godwits, particularly those relating to certain parts of the nesting cycle on which my own notes are thin. In addition, I am indebted to Dr. Sally Hoyt Spofford for permission to use data on the incubation period and the behavior of adults at hatching time from a letter written to her by Dr. Arthur A. Allen in 1954.

Summing up the material available for this paper, I find that it includes direct observations on 14 nests with eggs, at least 30 broods of chicks, and upwards of 80 pairs of breeding adults. The base thus provided is relatively broad and, indeed, for some species of birds might be considered definitive. However, as will shortly appear, the ground activities of neither old nor young godwits are easily watched under the conditions which prevail at Churchill. In the case of the adults, I believe that some of this ground behavior will be found extremely significant when its details are verified and compared with the corresponding routines of other species of *Limosa*. Equally intriguing are the sequences in development of the young from hatching to flying, but these, too, need more field work.

In the circumstances, I limit this paper to a descriptive account of the nesting of the Hudsonian Godwit without attempting to follow up some of the leads which are presented.

Hudsonian Godwit Habitat

From the data in hand, it appears that nesting Hudsonian Godwits confine themselves to narrow bands of country which border, at some little distance, on tidal or fluvial shorelines. Moreover, it seems that this restricted distribution has been one of two major factors in prolonging the search for eggs and young chicks. For these reasons, a rather detailed consideration of the habitat at Churchill may not only explain a bit of past history, but also direct attention to other breeding grounds as yet unknown.

The physical geography of the Churchill region has been summarized from an ornithological point of view by Taverner and Sutton (1934) and in a botanical context by Scoggan (1959) and Ritchie (1962). The Ritchie paper is particularly useful: its maps of landforms and vegetational cover explain the visible landscape and provide a logical base for interpreting local distribution of birds. I have drawn freely on such parts of this material as apply to summer range of the godwits.

For a biologist, and many another visitor as well, the important fact about Churchill is its location north of the last straggling trees, on the edge of the great frozen plain called tundra. It is, indeed, the only spot on the lowland tundra of North America which may be reached by railroad. From The Pas, the town in west-central Manitoba which presently marks the limit of both agriculture and paved roads, a scheduled airline also spans the 500-odd miles to Churchill, but the railroad still has its advantages: if laid out for this single purpose, it could not better serve to introduce the Subarctic scene. Three times a week, at about nine o'clock in the morning, a long combination train pulls slowly out of The Pas station, crosses the Saskatchewan River, skirts Cormorant Lake, and at the end of an hour or so bears off northeast to follow the general course of the Nelson River toward Hudson Bay. All the remainder of that day it traverses a wide belt of boreal forest and, when the evening light finally fades, which is nearly eleven o'clock in June and July, the spruce trees on either side of the right-of-way are as thickly spaced, and as tall, as when the journey began. A short night follows, toward the end of which the brawling Nelson River is crossed for the last time at Kettle Rapids, and with the coming of another day the aspect of the country begins to change.

Twenty miles down the left bank of the Nelson, the rails turn rather abruptly from northeast to north, and henceforth point straight for Churchill, still some 150 miles away. Departure from the river assures, of itself, some change in the forest cover, for in the north country the streamsides are better drained than the bogs and muskegs which lie between and so support a thriftier growth of trees. However, other factors come into play as well: the land is lower and flatter; the indices of mean temperature decline; and not far ahead is the southern limit of continuous permafrost, beyond which only a shallow top layer of ground is thawed by the summer's warmth, while the subsoil remains hard-frozen. These are the factors which, in combination, retard and finally inhibit the growth of trees. In the next 80 miles the spruces are progessively shorter and farther apart, the bogs larger and the ponds and lakes more frequent, until at length, some 70 miles south of Churchill, the tracks lead out across a wide reach of all but treeless heath-lichen tundra on deep beds of peat.

This first stretch of tundra is known locally as the "false barrens" and not without reason, for it is only about 40 miles wide. To the newcomer, however, it demonstrates with some force that "treeline" in the lowlands is not a line, but a wide zone of change between two vegetative associations. Within this zone the factors which permit the growth of trees are in such delicate balance with their opposites that very small differences decide the issue: at one place, trees; at another place, no trees. So it is with the false barrens, for 30 miles south of Churchill the Broad River peats begin to shelve out against slightly higher upland of glacial drift, and the open tundra gives way in turn to larch bogs, to straggling outliers of spruce, and, presently, to closed spruce forest. At Mile 500 the train crosses a maze of tidal creeks flowing northwest toward the Churchill River, now close at hand, and for the next few minutes no denser woods, no taller spruces, have been in sight since the Nelson River was left behind. However, the interlude is brief, for ice-bound Hudson Bay lies just ahead. At Mile 505 the first grade crossing slips by, and almost at once the trees become shorter, more weather-beaten, many of them dying, some long dead. Suddenly the train is in the open again. To the east, the buildings of the military post cover the top and the near sides of a low rounded hill. To the west are wide river meadows and flats, strewn with erratic boulders large and small; beyond that the estuary of the river, three miles across when the tide is in; and on the farther shore, a ridge of rocky hills running up to 160 feet, the highest land for miles around. At half past seven in the morning, or thereabouts, the train arrives in Churchill.

Hudsonian Godwits are occasionally seen on the tidal flats of the estuary at Churchill, and in some years a pair or two may nest on the river meadows, but the ground where they are common lies to the southeast of the town. Two gravel roads give access in this direction, one seven miles in length, the other about 22. The shorter is the old road leading to the float-plane base and other facilities on Farnworth Lake—the "Landing Lake" of Taverner and Sutton (1934). It has been in use for upwards of 35 years with consequent disturbance to its surroundings. The more recent military road, already mentioned, runs some 12 miles east from the edge of town, two miles southeast, and eight miles south to Twin Lakes Hill, an isolated mound of glacial drift rising 50 or 60 feet above the surrounding tundra. The final eight-mile leg of the road passes through an almost complete series of the local vegetational types and, except for the gravel pits from which it was made, with a minimum of damage. It thus affords, by chance, an excellent synoptic view of godwit summer habitat.

Where the Twin Lakes road leaves Fort Churchill to wind down the easterly slope of the hill, there is a broad general view of the country which lies ahead. The coastline, here running in a gentle sweep just north of east, is marked by a series of rock outcrops rising from a gravelly plain, the nearest to about a hundred feet, those more distant successively lower. To the left of these black headlands lies Hudson Bay, frozen solid until mid-June, and for a month afterward covered by enormous fields of pack ice which come and go with each change of wind. To the right the plain soon merges into a wide belt of open marshy tundra which stretches away to the south, its surface dotted with innumerable pools, ponds, and lakes, until it meets and is presently absorbed by the ragged-looking spruce woods along the horizon. Here, laid out before us, is the basic zonation of this coast: tidal flats and foreshore, partly drained old-beach plain, poorly drained marsh tundra, straggling spruce-larch forest.

Leaving the Fort hill, the road leads out across the gravel flats, skirting or climbing over the southern flanks of the outcrops, and comes at the end of nine miles to a fork. On the way, there have been ponds and lakes on either side, three or four rushing streams which have cut down 10 feet or so into the permafrost, and on the left, views of wide coves and miles of tidal flats lying between the headlands. Also, if the time be June, there have been many pairs of American Golden Plovers by the roadside, for they reach their greatest density in the Churchill region on the drier parts of this plain. Northern Phalaropes swarm in every grassy pool, several other small shorebirds are common and the long trilling songs of Whimbrels float up from the south; but godwits are unusual along this stretch until mid-July when suddenly there are many pairs with their broods, crossing the road on their way to the shore.

Bearing right at the fork, the road now heads diagonally away from the coast, winds between more ponds and lakes, crosses the top of a low rock outcrop half buried in water-washed drift, bends back on itself, and presently crosses a stretch of flat tundra to the north end of a wooded gravel ridge, an old beach which it follows straight south for several miles. For part of the way the scraggly, widely spaced spruce trees restrict the view, but the ridge soon narrows and a wet marsh, fringed with low willow bushes, shows through the trees on either side. Stop here in the nesting season, and at once there are several godwits in sight overhead, and more calling in the distance. The road keeps on to the end of the ridge at about seven airline miles south of the coast, and thence crosses, on a raised causeway, some two miles of what looks to be a grassy marsh. Beyond the marsh lies a belt of open larch-willow swamp, and beyond that the spruce forest on the slopes of Twin Lakes Hill. There is no need to go farther than the willow belt because, in the three miles or so from

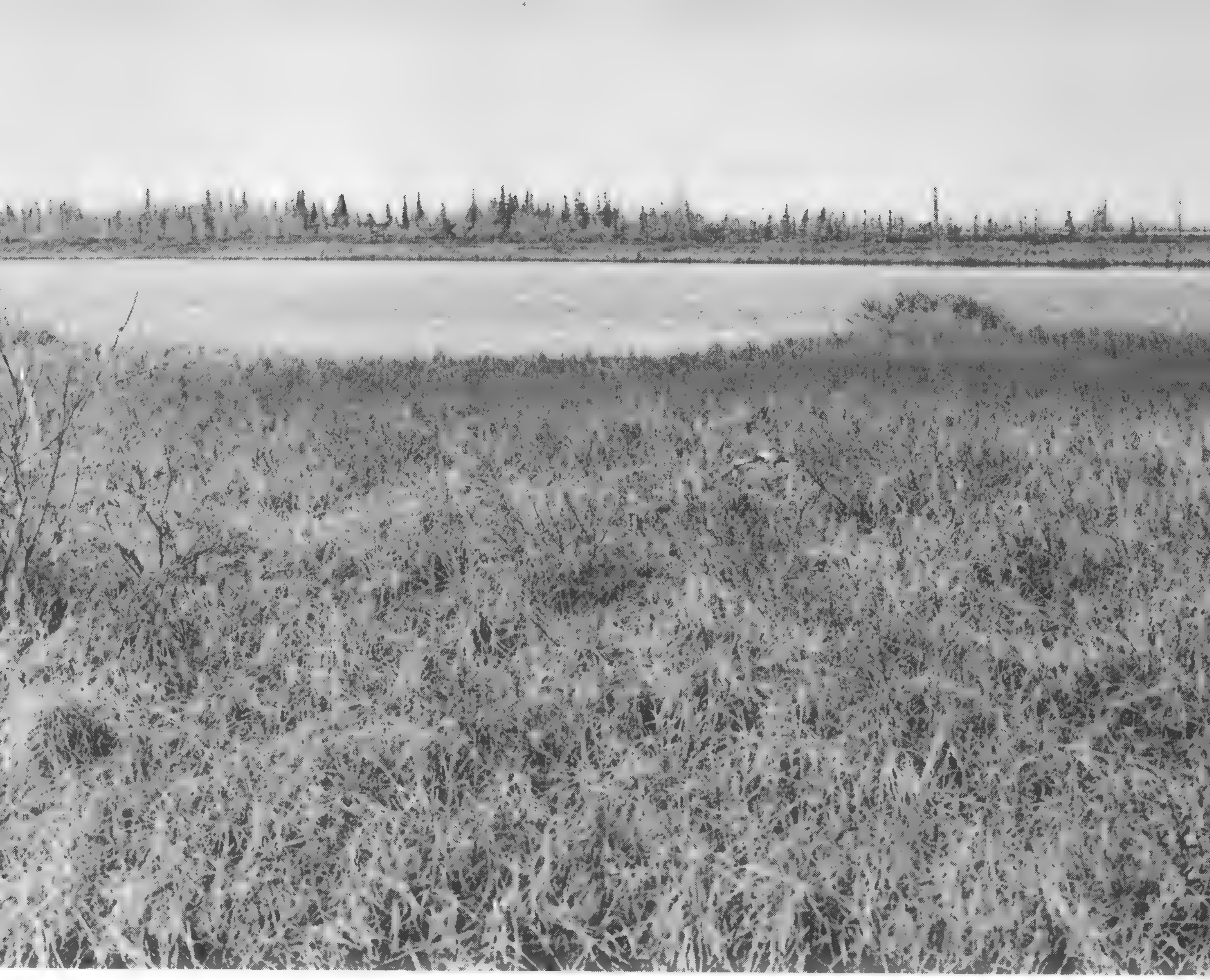


Figure 2. Site of a Hudsonian Godwit nest at Churchill, 24 June 1962. The nest is beside the bleached spruce branch, right of center in middle distance. Note the environmental mixture of sedge meadow, tundra lake, and straggling spruce-larch woods.

the first stop on the ridge, we have traversed, at right angles, the strip of country where Hudsonian Godwits nest in greatest numbers. Here, in June and early July, they are everywhere seen and heard: pairs and small groups scattered across the marsh among ducks of several kinds, Short-billed Dowitchers, Stilt Sandpipers, Dunlins, and the lesser shorebirds; and others in noisy display aloft, where their associates are Whimbrels, Common Snipe, and Lesser Yellowlegs.

And now, what is the special nature of this range? To begin with, it is back from the coast. This partly explains the long failure to find it, for traditional routes of summer travel in the Arctic are up and down the major rivers and along the shores between their estuaries. But why is it back from the coast, or more specifically, what are the conditions which restrict the distribution of Hudsonian Godwits on the Churchill tundra?

First there is a definite relationship between nesting strip and northern limit of tree growth. The latter is not easily defined, being very irregular, but in general terms continuous spruce forest approaches from the south within six to 12 miles of the Churchill-Cape Churchill coast. There it becomes discontinuous and breaks up into long fingers of scattered trees which push out across the tundra for another two or three miles, following gravel ridges and taking possession of other slight elevations which offer a toehold. Nesting godwits are almost wholly confined to the belt of country where woods and tundra intermix (see Figure 2), for we have seen none in the continuous forest to the south, where Lesser Yellowlegs are not uncommon around small openings; and until mid-July very few on the drier treeless plains toward the coast.

Next, as we examine the occupied habitat more closely, it appears that both its surface and its vegetation are much less uniform than the first glance suggested. This is not unusual on the tundra, where the rather forbidding sameness of the whole landscape may mask an unexpected diversity of detail, but here the variation becomes striking. It begins with the differing proportions of trees and tundra: to the east of the Twin Lakes causeway are vistas which stretch away to the far horizon, with nothing more than scattered spruces and small tamaracks to catch the eye, while westward the open land is so broken up by irregular patches of woods that only intervales of meadow remain. Clearly there are low elevations to account for the trees, and a foot-traverse in any direction soon shows that differences of level extend across the open country as well. Within a vertical range of four or five feet at the most, the surface is rough and hummocky beyond description. Moreover, because permafrost retards the development of a drainage system, every depression holds water. The result is a very great number of ponds, from small to large, and no one of them at the same level as others nearby; and over all the remaining surface, on sites which vary from wet marsh to dry barren, is an intricate mixture of sedges, flowering plants, low shrubs, mosses, and lichens.

The open-water ponds and lakes tend to be rounded in shape and are rimmed by natural dikes which have been pushed up, over long periods of time, by the forces of expanding ice in early winter. Their sides, from the same action, are usually perpendicular walls of solid peat; less often, narrow sloping beaches of desiccated peat. Their bottoms are hard level pavements of rock shingle, and when the spring flood has subsided, these ponds have an almost uniform depth of about two feet. Most of them can be waded from shore to shore even where the distance is as much as a mile. Except that a young bird now and then escapes some predator by swimming, the ponds hardly figure in the life of a godwit.

The meadows and moss barrens actually used by the nesting godwits occupy a vertical range of perhaps two or three feet, lying between the level of standing surface water and the edges of the spruce woods on the gravel ridges. The plant cover is surprisingly rich in species because the roughness of the ground implies constant change of height above the nearest water—i.e., the vegetation on even a small hummock ranges from emergent aquatics around its base to lichens across its dry top. Nor would it be easy to exaggerate the intricacy of this diversification over the length and breadth of the nesting belt, for no marsh or meadow is without its raised nubbles and mounds of every shape and size; no dry barren without its wet depressions. But further analysis of the vegetative cover is work for a botanist; in this paper, a simplification into three dominant types will do.

Sedge marsh is the important wet component in the habitat, accounting for 12 to 18 inches of vertical range and 40 to 60 per cent of total surface. Several genera and many species are represented in the sedge complex at different elevations, with growth short and sparse in the six inches of standing water at the lowest levels, progressively taller and thicker in lesser depths at higher levels, and toward the top of the sedge range, where the spongy peat soil shows water only under pressure, so coarse and luxuriant that it becomes more hay-meadow than marsh. Adult godwits find the bulk of their food in the wetter parts of the marsh during the nesting season—which means, in fact, that they spend all of their time there when not displaying or incubating; and thither the young birds are led soon after they hatch.

Second in area, but supplying only one essential of godwit existence, is moss-lichen barren. The term is here used in a limited sense to designate tundra raised above the level of standing water and comparatively dry. When so defined, a barren may be many acres in extent or no more than the top of a small mound, the plant associations being similar. While mosses and lichens give their name to the type, the dense springy mat of vegetation which covers the surface includes an amazing variety of other plants. Ericaceous shrubs of several genera, all extremely dwarfed, are a prominent element, in particular the tiny Lapland rosebay which dots the barrens with bright color when it blooms midway of the shorebird nesting season. Dwarf birch is also very widespread, although its prostrate habit and lateness in leafing out render it inconspicuous. With rare exceptions, godwit nests are placed in the moss-barren vegetation on the tops of hummocks surrounded by sedge marsh and meadow. Larger areas of barren may serve as escape cover for young godwits which have been feeding in nearby depressions, but this is incidental.

Willow swamp is the least of the three types in area, but not in use. Unlike the other two, it is present only as a belt of varying width which borders gravel ridges and other elevations. Its clumps of willow bushes are widely scattered, its sloughs knee-deep with peaty bottoms, and its outer edge merges irregularly into the mixed sedge marsh and moss barren of the open tundra. It is this transition zone which seems particularly attractive to godwits, and its hummocks and islands probably carry the maximum density of nests. This willow swamp also provides early rearing cover for the chicks hatched there, during the two or three days before they venture farther afield.

The final step in describing godwit habitat is to consider again its relationship to the coast. We have seen already that it lies among the last straggling spruces on the edge of the open tundra. In the Churchill River valley the trees approach within two or three miles of the coast, but eastward they recede by degrees until the nesting birds are 10 to 12 miles inland. Accordingly, if it were not that other data, as yet scanty, suggest a further limit, we might infer that the treeline cover type is the controlling factor, without regard to distance from the coast. The first bit of negative evidence is the absence of nesting-season reports of godwits from the edge of the false barrens 30 miles south of Churchill where ecological conditions appear much the same as in the occupied strip. Again, there are no records from any point in the treeline zone which wanders northwestward from Churchill across the interior of southern Keewatin and eastern Mackenzie. On the positive side, every nesting of the species thus far reported is within 50 to 60 miles of tidewater, or less if "tidewater" includes such rivers as the Sutton, Winisk, and Anderson, where apparently the occupied ground bears somewhat the same relationship to the river banks as it has to the coast at Churchill.

I conclude, then, that the likely essentials of Hudsonian Godwit range are extensive sedge marshes and meadows lying in the northern edge of treeline and not far from a tidal coast.

Arrival of Godwits on Breeding Grounds

Spring comes to the tundra with dramatic speed, for a sequence of events which spreads over two or three months in temperate climates is here compressed into a period of days. The ornithologist is among the first to feel its impact because birds are so visible and audible a part of the change. A condensation of my notes for the first days of June 1962 records the arrival of godwits and other shorebirds and suggests, I hope, the feel of spring at Churchill.

> *31 May.* Cold and raw, northwest wind drawing to easterly, temperature 29-33°F. Deep snowdrifts in the woods, in every lee of ground, and banked high against the houses in town; many bare spots too, and pools of meltwater in depressions ashore and on the solid ice of the river. Hundreds of Horned Larks, Lapland Longspurs, and Snow Buntings about the townsite, but, except for two pairs of noisy Killdeers, not a shorebird to be found.
>
> *1 June.* Wind southerly in forenoon, and sun, after breaking through rifts in overcast, shone warm during middle of day; by late afternoon wind drew to northeast and freshened, temperature falling rapidly as chill from Hudson Bay ice came over the land. Snow melted fast in town, more slowly back from the shore. In late forenoon to Twin Lakes Hill and saw the first American Golden Plover 10 miles east of town, but as soon as the road turned south, away from the bay, the tundra lay deep in snow: no birds but longspurs and buntings, occasional Pintails and Canada Geese on pools of meltwater, and a Snowy Owl. Back to town, and by 4:00 PM shorebirds had begun to arrive — three Semipalmated Plovers, six Ruddy Turnstones, three Semipalmated Sandpipers, and a Stilt Sandpiper on the townsite slough by early evening. Circumstances of arrival much the same for all: we heard birds calling overhead, looked up to see them pitching down on steep slant; they circled the slough, calling repeatedly, and within a minute or two dropped into some sunny spot out of the wind, tucked heads into scapulars, and went to sleep, not to move again for as long as we watched. A Bonaparte's Gull, too, asleep on a rock in the slough.
>
> *2 June.* Wind southerly from daylight, and sun warm until early afternoon, when light overcast closed in from west, thickened slowly, and was followed by rain at 5:00 PM. No sooner up than we discovered townsite alive with larks, longspurs, and buntings — thousands where there had been hundreds two days before, and the first Tree Sparrows singing. Out the Farnworth Lake road in forenoon to find same transformation: Lesser Yellowlegs yodeling over the spruce woods in every direction, Semipalmated Sandpipers well scattered and already beginning to sing, male American Golden Plovers chasing each other by twos and threes, Short-billed Dowitchers and Stilt Sandpipers coursing over the tundra, Semipalmated Plovers common, the first Whimbrels, and two single Hudsonian Godwits – a bright male in flight, a female probing the edge of a marshy pool. Most of these birds appeared to be already on territory, while others, in flocks, were either just arriving or were transient: a flock of 15 Golden Plovers which lit for a moment only and then kept on to the east; several small flocks of Stilt Sandpipers pitching down from high overhead to alight on the borders of tundra pools; many small wisps of Semipalmated Sandpipers and a flock of a dozen dowitchers pressing eastward across the tundra. By late afternoon, at the townsite slough, the first Northern Phalaropes had arrived, and a flock of 25 White-rumped Sandpipers swirled in from the south, lit on a sand bar, and soon fell to feeding.

3 June. Another spring-like day: seven hours of bright sunshine from midforenoon to late afternoon, but fresh southeast wind off the Bay kept air temperature in the 40's. Out the Twin Lakes road in afternoon; less snow and more open water on the tundra, but still the landscape more white than brown. A great influx of shorebirds in last 24 hours: Semipalmated Plovers, Whimbrels, Dunlins, and Least and Semipalmated Sandpipers, and particularly Hudsonian Godwits, nearly or quite as common and widely distributed as they were ever to be later, although much of the ground on which they would actually nest was still under snow or water. Least Sandpipers and Dunlins had arrived in a flood overnight, many Common Snipe were bleating overhead, and male American Golden Plovers greatly increased on dry tundra. In addition to territorial birds, many transients hurrying by to the eastward: Semipalmated Sandpipers and Dunlins in flocks of 10 to 40, and smaller numbers of American Golden Plovers, Whimbrels, and godwits.

4 June. Overcast in forenoon, but a sunny afternoon with temperature near 60°F in sunny lees, while southeast wind kept air chilly; snow melted fast during middle of day. Common Snipe arrived in force during previous 24 hours, and many winnowing overhead along the Farnworth Lake road. Whimbrels conspicuous too, their long trilling flight-songs coming from every direction, but other territorial species less noisy, as though the first flush of spring exuberance exhausted. Migration of Semipalmated Sandpipers and Dunlins continued unabated, with a few White-rumps and the first single Black-bellied Plover mixed in.

5 June. Heavy ground fog early and late; sun shone from 10:00 AM to 3:30 PM back from shore, but a biting cold wind blew from the bay. To end of Twin Lakes road, and on the way found that female American Golden Plovers had either arrived en masse or had dispersed from flocks; there were now pairs where formerly little groups of males. Also, a general arrival of Northern Phalaropes. Godwits displaying more frequently, but still spend most of their time feeding and sleeping. Eastward migration much reduced.

6 June. Increasing overcast, with rain in early afternoon and not clearing until nearly sunset (9:15 PM), but for first time in a week almost no wind so that the penetrating chill from the ice-locked bay was gone, the air pleasantly warm. After lapse of one day, shorebird migration resumed on larger scale than ever, with occasional small flocks of American Golden and Black-bellied Plovers and Knots among the much greater numbers of Dunlins and White-rumped and Semipalmated Sandpipers.

7 June. Fog until midmorning, followed by clear afternoon with warm sun and temperature near 60°F. Out the Twin Lakes road at noon and found great changes: deep drifts of snow on ridges shrinking fast, tundra now brown where it had been white, ponds and lakes mostly open. Marked effect on birdlife: pairs of Arctic Loons on larger ponds, Willow Ptarmigan suddenly common and conspicuous on the mosses, Lapland Longspurs literally everywhere, their tinkling flight-songs showering down from overhead and the birds themselves chasing each other hither and yon. Adding the final touch of animation, groups of phalaropes twittering and chasing in every pool, and snipe, Whimbrels, Lesser Yellowlegs, dowitchers, godwits, and several smaller shorebirds "singing" and displaying in the air above.

Thus, in a week's time, the tundra is transformed from winter to summer. The foregoing notes touch on the main aspects of shorebird arrival and, with an added comment or two, will sufficiently cover the subject in respect to godwits.

Several previous observers (e.g., Bailey, 1948:200) have noted that, on the tundra, first-arriving shorebirds appear suddenly—often overnight—and are already dispersed when found; they are followed within a few day by flocks of the same kinds which push on to the north. Working backward, it may be inferred that the birds which will nest locally are the first to come, and their flocks—for the tundra-breeding species all migrate in flocks—tend to break up within a few hours at the most, which makes their arrival unobtrusive. In contrast, birds headed for more northern nesting grounds remain in flocks, and their passage is thus conspicuous.

The arrival of Hudsonian Godwits at Churchill fits this general pattern if it turns out, as now seems probable, that the species does not nest farther to the northeast or north, but only at points on the Mackenzie coast which are reached by routes lying west of Hudson Bay. In the afternoon of 3 June 1962 I saw one flock of eight godwits which I thought, from their behavior, were just arriving. On 28 May 1964, Jehl noted a small flock and a flock of 42 the following day, but in 1965 saw no flocks at all. By and large, the moment of arrival is not often observed.

Many arriving shorebirds seem to be tired, as noted under 1 June above, and in some species, including godwits, the appearance persists for a day or two, as shown by long sleeping periods and infrequent displays. On the other hand, it appears that Lesser Yellowlegs are active and noisy from the first morning. The contrast suggests that the muskeg-nesting yellowlegs have traveled by stages across country suited to their requirements, while the tundra-nesting birds arrive by long flights from the prairies.

Voice

Of northern-hemisphere shorebirds, perhaps none are more silent than godwits in migration and few so noisy on the nesting grounds. At Churchill, the Hudsonian Godwit well fits the generic pattern, for if Whimbrels and Lesser Yellowlegs account for larger shares of the general volume of bird sound on the tundra, it is only because of their moderately greater numbers. The other shorebirds, although they "sing" persistently, are overshadowed by these three.

Godwit calls are expressive, and at first hearing I thought they included a wide range of distinctly different sounds. On longer acquaintance, particularly as I noted how one call merged into another, this impression faded. My present opinion is that the godwit repertory is rather simple in structure: a basic disyllable, modified by fleeting changes of pitch and clearness of tone, and by accent, volume, and the speed and intensity of delivery, to produce all the calls which are associated with the excitements of the nesting season. The common variants make up two loose groups, interrelated in both form and function, of which one is associated chiefly with display activities during the first month of the breeding cycle and the other chiefly with guarding of young birds during the second and final month.

The display group stems from the *toe-wit, toe-wit, toe-wit* which is thought to have given the godwits their vernacular name. The call itself is pitched at 3,000 to 5,000 cycles per second and is relatively clear in tone. Its variations are in the direction of increasing accent and force of delivery. The simplest form, used intermittently when feeding, bathing, or preening on the ground, is unaccented, not loud, and a bird giving it does not appear excited. A low-intensity flight form has the second syllable accented, volume increased, delivery still discontinuous but in longer series at an average rate of one call per second, and some appearance of excitement. This merges into a high-intensity flight form with accent and volume further increased, and calling continuous at a rate of 60-110 repetitions per minute. At this point a connecting syllable is often added to give *toe-wit′-ta-toe-wit′-ta-toe-wit′-ta,* and this in turn may be smoothed out into *wur′rity-wur′rity-wur′rity-wur′rity.* This last variation is heard rather infrequently and always, in my experience, from high in air; it has a mellower tone than the common *toe-wit, toe-wit.* Although lower in pitch, it suggests, and is apparently analagous to, the yodeling songs so persistently used in the nesting season by Willets and the two species of yellowlegs.

The protest or guarding calls of the Hudsonian Godwit also stem from *toe-wit,* or more exactly from its second syllable, which is aspirated to become the important element of the group. The simple form is *whit, whit, whit* delivered with rising inflection and the stop effect of the final *t* sharply emphasized. This is regularly expanded to *whee′-wit,* the first syllable with rising inflection and strong accent, the second falling very slightly to the same sharp stop as in the simple form. Less frequently — and I think only by some individuals — there is a further expansion to *whee′-wee-wit,* or again to *whee-wee-wit′.* Protest calls are always accompanied by some appearance of anxiety, and their usual range of intensity and volume is from moderate to high. In the ordinary sequence, any disturbance in the vicinity of chicks elicits from the guarding parent a series of disconnected *whit*'s, four to 10 a minute. As the supposed danger comes nearer, volume of sound, continuity, and speed of delivery are rapidly stepped up to a ringing *whit, whit, whee′-wit, whit-whit-whit-whit-whit whee′-wit* at a rate of 60 or more calls per minute. This pitch of calling entails no little effort, for each repetition of *whit* or *whee′-wit* is accompanied by three movements: a quick, almost convulsive, retraction and extension of the neck; a counter-balancing flick of the tail if the bird is on the ground or a tree-stub, or of the legs if the bird is flying; and, as the sound issues, the bill is opened so that the tips of the mandibles are about three-quarters of an inch apart. This rather unusual profile is shown in the accompanying wash drawing (Figure 3) by Dr. George Miksch Sutton.

In addition to the common calls, there are two little-used variants which express the extremes of excitement in the guarding of young birds. One, which for the first few days calls in the downy chicks for brooding, is a soft *cuck-cuck-cuck-cuck-cuck,* chattering or conversational in tone. The other, used in the last moment of frenzy as a predator or human intruder catches or picks up a chick, is a grating, rasping squawk, almost incredibly loud and harsh to come from a bird not quite as large as a pigeon.

By way of rounding out this description of Hudsonian Godwit calls, two comments may be added. The first has to do with the marked resemblances between the calls of all the godwits. In addition to hearing three of the four species of *Limosa* calling in life—*fedoa* at various times in Minnesota, North Dakota, and Manitoba; *haemastica* at Churchill, *limosa* at Tipperne on the North Sea coast of Denmark—I have listened many times to tape-recordings of *lapponica* on file at the Cornell Laboratory of Ornithology's Library of Natural Sounds. From this evidence, I conclude that an observer who knows the voice of one species will almost certainly recognize, as coming from a godwit, the voice of any other species. Several small differences will bear further

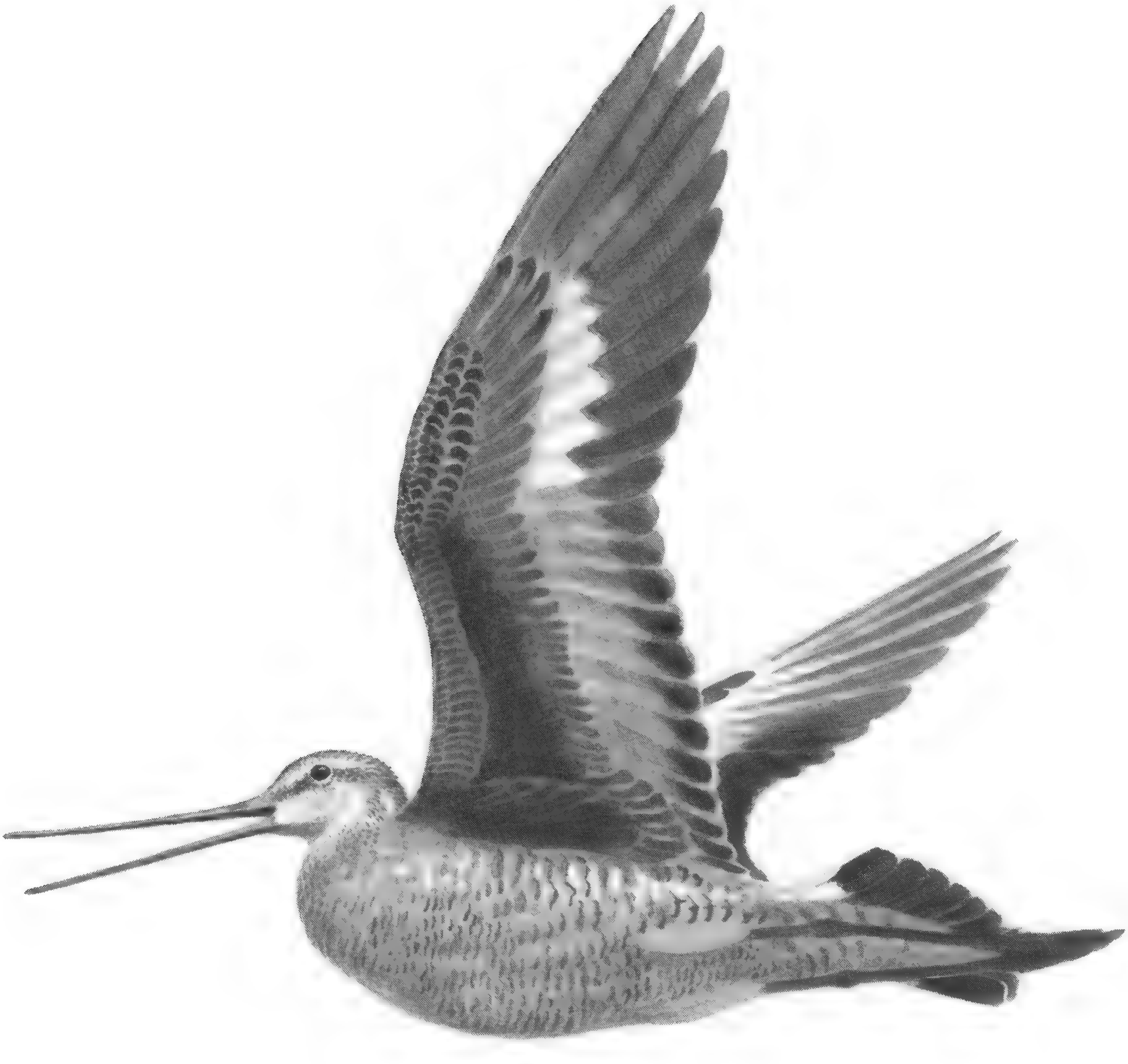


Figure 3. Female Hudsonian Godwit protesting an intruder at her nest in June. Her bill is open and her neck retracted as she gives *wheé-wit* call. Note that her feet extend behind the spread tail. (Drawing by George Miksch Sutton, from a photograph by the author.)

study for their possible taxonomic significance, but in general it is the similarities which are really striking.

Finally, I would re-emphasize the extreme fluidity of Hudsonian Godwit calls within their given framework. Not only does one call become another, abruptly or by degrees, but each in itself is used with constant changes of volume, rapidity, inflection, and, particularly, of tone to express different levels of excitement and involvement. The godwit voice, ranging from mellow to shrill and harsh, never falls so sweetly on the human ear as that of American Golden Plover or trilling Whimbrel, but it is far more variable and, thus, more expressive.

After a week or two of listening to the calls, it is possible to stand on the tundra, eyes closed, and have a very fair idea of the current activity of every godwit within hearing.

Forms of Display

Shorebirds as a group are much given to aerial displays, accompanied by persistent "singing" of one sort or another, and godwits rank among the most conspicuous performers. Since the Hudsonian Godwit is by nature a strong flier, ranging far and wide above the tundra and inviting attention by its noisy calling, the observer will be familiar with these displays long before he has an equal acquaintance with ground activities. The flights are of two general sorts: a song-flight, by males alone, in which the vocal element is prominent; and pursuit-flights, usually involving a female and one or more males, to which the calling is somewhat incidental. Both are presumably territorial, but for the moment I confine myself to their forms, leaving the question of function for later consideration.

Description of a typical song-flight must begin with the fact that a male godwit, even in June, spends most of his time feeding along the edge of some shallow tundra pool, where every move he makes has an air of quiet, methodical industry. Early in the month there may be a female nearby, similarly engaged and, at greater distances, other pairs and single males, but for long periods each bird seems engrossed in its own probings. From this setting, a song-flight is sometimes triggered by the calls of another godwit overhead. Quite as often there is no discernible reason for it. The bird looks up abruptly from its feeding and in the next moment is on wing, going up a long incline with strong deep strokes and giving the low-intensity call, *toe-wit, toe-wit, toe-wit*. When this first straight run has carried him 100 feet or more above the tundra, he falls silent and begins to climb more steeply by a series of irregular spiral circles and figure-eights which may be small or large. At a height of six, seven, eight hundred feet, he straightens away again on a level run with wing-beats normal, body rolling slightly from side to side, and intermittent bursts of *toe-wit′, toe-wit′* increasing by degrees to medium intensity. On this run he may soon swing into a wide circle, or he may go half a mile before he turns, but, whatever the course, he is presently back in the vicinity of his starting point, the intensity of his calling steadily increasing as the distance shortens. A moment later his wings no longer lash the air, but are held, fully extended and rigid, at an angle of 45° above the horizontal, while he glides in wide irregular circles, pouring out the high-intensity *toe-wit′-ta-toe-wit′-ta-toe-wit′-ta-toe-wit′-ta* as he slowly loses altitude. At intervals he waves his wings with exaggerated slowness in a narrow arc between 30° and 60° above the horizontal. A minute or more goes by without the slightest break in the calling, until suddenly it stops short and he points his bill straight down, closes his wings to his sides, and drops like a stone—down, down, down. No more than 40 feet above the ground he extends his wings, very slightly until they brake his speed and then more fully, traces a smooth curve from vertical to horizontal, and glides gracefully to a landing on some bare tussock. As his feet touch, he raises his wings straight up, flutters them quickly at the tips, and folds them deliberately, one a bit ahead of the other. At this moment the female frequently comes in low across the tundra, lights nearby, and both birds fall quietly to feeding or preening. Twenty minutes or more will usually go by before another flight.

Within the general pattern, song-flights of different males and successive flights of one male show many variations. Not uncommonly in middle and late June a display will either begin or end with an attack on some passing hawk or jaeger. I have mentioned that one bird may describe a wide circle in the pre-climax phase of the flight, while another goes straight away above the tundra until he is nearly lost to sight and hearing. My field notes describe a male which called *toe-wit'-ta-toe-wit'-ta* without a break for two minutes and a quarter and several others which called for a minute and a half. Sometimes a bird, at the end of his flight, lights on the top of an isolated spruce or larch (Figure 4). The calls of different birds vary in all the ways previously noted, and particularly in a tendency by some to soften their voices to a sweeter, more mellow tone at the climax. But these are all minor differences; on the whole, the song-flight is strongly ritualized.

Consider, for a moment, how every striking feature of the breeding plumage is emphasized at some stage of the flight. With the first calls, the opening and shutting of the bill attract attention to the flame-orange base of the lower mandible. During the rise the widely spread tail shows off the contrasting black and white of its upper surface, and in level flight the slight rolling of the body accents it, now on one side, now the other. In slow circling at the climax, with wings held up or waved, the dark axillars and under-coverts are outlined against the lighter color of the flight feathers, particularly the white bar on the inner primaries. As the bird noses over into the vertical drop, all the black and white contrasts—tail and wings, upper and lower surfaces—are abruptly hidden from the moment the calling stops. At the bottom of the plunge they flash into sight again with the opening of the wings. And in the final pose on the ground, where the solid chestnut-red of the underparts is seen to better advantage than in the air, the flutter of the wings is remarkably effective in drawing the eye. Many times, in the course of searching the tundra with glasses, I have caught the quick black-and-white twinkle which told me of a lighting godwit, too far away to be noticed a moment later when his wings had been folded.

Pursuit-flights, from the observer's point of view, are a display of wing power rather than plumage, for they are carried out at headlong speed with many twistings and turnings. Another way of introducing this distinction is to say that the birds themselves seem wholly intent on the chase and strike no postures which call attention to their markings. Pursuit-flights are also somewhat less stereotyped than song-flights, which makes for difficulty in selecting one sequence as more "typical" than another. However, as chase after chase is watched over a period of days, certain details recur many times, so that in due course a general pattern takes shape.

The start of a pursuit-flight, as of a song-flight, is abruptly spontaneous. It may be set off by the calling or near approach of another godwit, but quite as often there is no visible releaser. Nearly always it begins with what appears to be a mated pair and, although the action is too quick to be sure, I have the

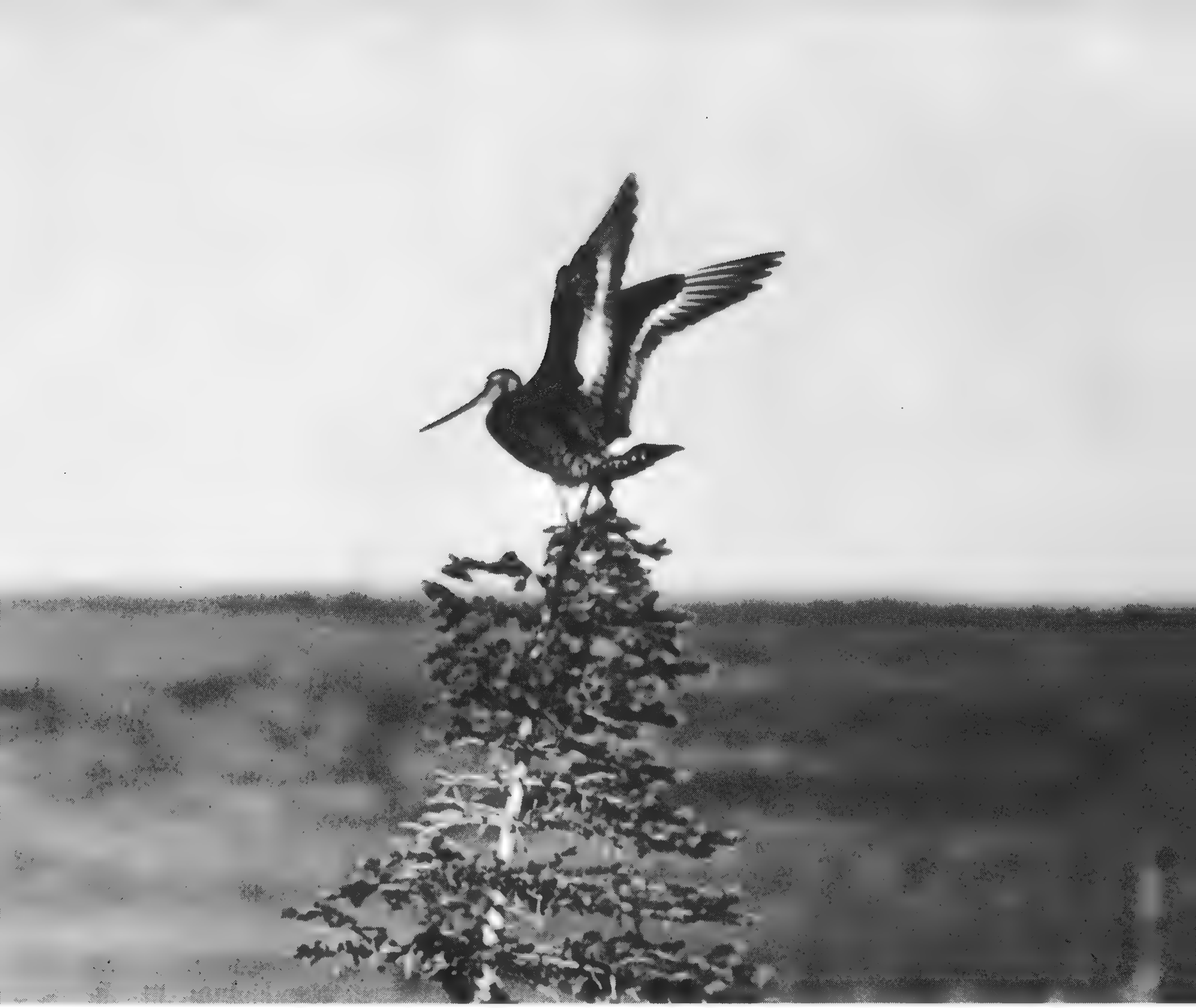


Figure 4. Male Hudsonian Godwit alighting on a treetop. His wings are held up a moment before deliberate folding.

impression that the female is the first off the ground. At any rate, both birds are up in the wink of an eye, the female zigzagging from side to side, yet not deviating far from a straight course; the male no more than a length behind, following every turn and calling *toe-wit′, toe-wit′, toe-wit′* in ringing tones. The initial rush is usually low over the tundra, and in many cases goes no higher; the two soon light again not far apart and immediately begin feeding or preening without further excitement. But if not thus aborted, the flight now takes a more spectacular turn; the female starts to climb, the male follows closely and, when they are perhaps a hundred feet in the air, other males begin to rise from near and far to join them. Away they all go across the tundra, zigzagging and twisting, rolling from side to side with spread tail in the turns, their wing strokes deep and strong, the males all shrieking *toe-wit′, toe-wit′, toe-wit′,* the female silent. The original pair may go almost out of sight or may swing in a very wide circle, but their retinue changes continuously: when each of the joining males has flown three or four hundred yards, he peels off and scales back to near his starting point, while another rises ahead of the chase to take his place. How many birds may be involved in a pursuit-flight depends on its length and on the density of the surrounding population, but two or three extra males at one time is not unusual, nor is a total of eight or 10 during the course of a half-mile circuit of the neighborhood. The end of the flight is usually as abrupt as its beginning: the pair return to the general vicinity of their departure point, light quietly, not always near together, and are at once absorbed in feeding or preening.

Although pursuit-flights are extremely variable in their details, none of the variations seems to be particularly significant. My notes contain one observation of an early-June chase in which two males, apparently competing for the attention of a female, repeatedly spurted in front of her; but since we never saw another pursuit in which the female did not retain the lead throughout, I attach no importance to it. Again, we have one record, and only one, of a male chasing another from his feeding ground.

The variations which do occur commonly are in the number of birds involved, the duration and intensity of pursuit, the height above ground, the noisiness, and, perhaps most conspicuous of all, the different ways in which flights start and end.

Territoriality and Ground Displays

Of the several parts of this paper, the present section must be the most tentative in its statements, for the data so far gathered do not answer many questions about those routines which are usually included under the heading of "courtship." Some of the indications of territoriality in a bird species are competitive display or hostility directed at other males by a male establishing or maintaining a territory; regular attendance by the male or the pair on the territory; mutual displays between male and female leading to selection of nest-site and to copulation; and, in many cases, a definite spatial relationship between territory and nest. During June 1962 we devoted the major part of each day to watching Hudsonian Godwits, and on several days kept one or two pairs under continuous observation for a number of hours, but with meager results: we were never able to identify the limits of any territory, noted only one instance of friction between adjoining males, only a single copulation late in the season, and no ground displays of any sort either by a male or a pair. Accordingly, I can do no more than sketch in a framework of description for the first weeks of the nesting season and leave the details for the future.

The greatest handicap in watching Hudsonian Godwits is their tendency to range far and wide across the tundra. Display flights are extended and, although the original participants usually return to the vicinity of the starting point, they fairly often pitch into a different part of the marsh, thus breaking the continuity of observation. In similar fashion, a pair may be found in a certain part of a marsh for several days in succession and seem to be settled there, only to be gone on a later day. Hardly less frustrating to the watcher is the quiet demeanor of birds on the ground and the lack of any sequel to either a song-flight by the male or a pursuit-flight by both. Except for flight displays, methodical probing for food is the major activity of both sexes from the day of arrival to the beginning of incubation, with sleeping and bathing a poor second and third. Even the song-flights of the male are much less frequent in early June than later in the month.

Three incidents condensed from my field notes will point up some of the difficulties in watching godwits during June and also put on record my only observations of possible territorial conflict and of copulation. The first concerns a pair which probably had, on 14 June, an incomplete clutch of eggs. In walking across an area of diked wet tundra, where the ridges rose perhaps 12 to 15 inches above the water, I looked up to see a female godwit coming straight toward me, low to the meadow, from about 35 yards away. She turned as I raised my head, went off eastward behind higher ground, and did not return. However, something about her sudden appearance had made me suspicious of a nest and, going to the approximate spot, I began a systematic search. Two or three minutes later, on looking up again, I discovered a male godwit watching me quietly but intently from the top of a four-foot spruce tree growing on a mound of peat. Here he remained for all of 25 minutes. When my widening circles gradually brought me within 20 yards or so of this bird, he took wing without a sound, flew across an open pool, and lit in its grassy edge, still only about 45 yards away. For a few moments he went through the motions of feeding without seeming to find much and then waded out in the pool to his belly and began to bathe, fluttering his wings vigorously to splash water over his back, bending forward to submerge his breast and lower neck, shaking himself until the drops flew, and finally dressing his breast feathers a few at a time by drawing them through his bill, which he repeatedly wet by dipping. As my search brought me again within 20 yards, he took wing and flew off in the same direction taken by the female, but lit on the top of a taller spruce before he reached the high ground. From here, in the next 20 minutes, he twice came back at no great height, circled me at about 40 yards, called *whee′-wit* in a low voice, and went off again, the second time going from sight where the female had disappeared. Two days later, I spent an hour in further search of the same ground without seeing or hearing a godwit. At the time, I supposed they had just moved elsewhere as others had done earlier, but in retrospect it seemed likely that the female had begun to incubate in the interim, for by 10 July a pair were guarding chicks in this same spot. The point of the story is the immediate removal of the female from anywhere in the vicinity of her first appearance on 14 June and the subsequent departure of the male after a show of mild concern which lasted more than an hour.

The instance of territorial conflict concerned two males which we watched for six hours on 17 June. One of them spent nearly the whole time feeding industriously in the grassy north half of a shallow pool which was divided across its midportion by some clumps of sedge; the other male had a more extensive range down the marshy shore of an adjacent lake, but twice came into the south end of the divided pool. On the first occasion, it called *whee′-wit, whee′-wit* at some little distance, and then more continuously as it scaled in on down-set wings to alight. The north-end bird raised its head, answered once from the ground, rose on wing, and closed quickly with the intruder; a furious pursuit-flight followed, both birds calling excitedly. When they had crossed the lake and swung wide over the tundra on the west side, the south-end bird lit on the tip-top of a spruce tree, and we saw that the other had transferred its hostility to a Marsh Hawk which was coming back across the lake. Hawk and godwit soon disappeared behind us, and 10 minutes passed before the latter reappeared, pitching in from the east without a sound, walking around for a minute or two with his head up, watching, and then going back to his endless probing in the mud. Shortly afterward, the south-end bird also returned, but this time silently; it scaled in over the tundra, lit, and for the best part of an hour the two fed quietly at opposite ends of the pool, apparently oblivious of each other. What finally broke the calm we failed to see, but suddenly the north-end bird took wing, flew the length of the slough calling *whee′-wit, whee′-wit,* and away they went down the lakeshore in another hot chase which ended when they lit on a bit of sloping beach, engaged in a brief tussle of some sort, and immediately separated. The north-end bird came directly back to the pool for another long interval of feeding.

At length it flew to the top of a 20-foot spruce behind us, sat quietly for a few minutes, and the next time we looked, was gone. Fifteen minutes later a godwit pitched in from the same direction, lit, and began to feed over the same ground as before. When we leveled our glasses on it, we saw it was a female. Too late, we realized that a nest-relief had been completed without our knowing it was under way. Afterward, it seemed probable that the south-end male had also been one of an incubating pair. We later found that the persistent feeding we had watched was normal male daytime activity at this stage of the cycle.

The copulation sequence was seen on 24 June, so late in the season that the female may have already lost her first set of eggs. I had been watching a female and two males feeding together in a marshy spot, when suddenly she took wing, followed closely by the males in a typical pursuit-flight. Within a hundred yards their calls had reached the high-intensity level — *toe-wit', toe-wit', toe-wit'*—and in a moment more one of them broke away to begin a song-flight at no great elevation above the tundra. The second male continued briefly in straight flight after the female, but soon veered off and lit far out on the marsh. As he left, she swung in a wide circle, came back toward me, scaled down on set wings toward an open pool, changed her mind, and lit on the topmost spike of a 20-foot spruce tree a gunshot away. The first male was by now waving his wings in slow motion at the climax of his display, but instead of pitching to the ground as he stopped calling, he resumed normal flight and came directly toward the female. He approached her from above and behind as she tilted forward and raised her tail, and, fluttering his wings to sustain his weight and balance, effected coition with great dispatch. In less time than it takes to tell, they were both back in the marsh, probing for food.

With regard to a relationship of the nest to occupied or defended territory, we found no substantial evidence. In some cases, particularly where a single pair nested in a small meadow somewhat hedged about by spruce woods, the non-incubating bird was usually, but not always, to be found nearby. On the other hand, of pairs located along the edges of extensive open tundra we had various observations to indicate that the off-duty bird was feeding far out in the marsh, often beyond sight or hearing of the nest. The extreme instance of this, which we saw by merest chance, concerned a nest between the military post and the river. For several days we had been watching two or three pairs of godwits which fed quite regularly in pools at the south end of the airfield runways but went far to the west and northwest when they left. On the early morning of 19 June, while driving out from town to Farnworth Lake, we were about three-fourths of a mile from the runway pools when I stopped to put my glasses on a passing jaeger. This done, I casually swept the southern horizon and immediately picked up a pair of birds coming toward us a gunshot in the air. They soon passed almost directly overhead: a pair of godwits with the larger female leading, the smaller male behind. Curious, but not anticipating the outcome, we held our glasses on them until, some quarter-mile beyond us, the female set her wings, scaled down to the tundra, and lit at a place where I had previously suspected a nest. The male, meanwhile, swung in a circle without lowering, came back by us, and presently went down in the vicinity of the runways. If not provable, it seemed at least likely that we had seen a female, accompanied by her mate, returning to her nest to lay an egg or to continue incubation. Whether or no, the incident points up the wide range of godwit activities, for the distance involved was well over a mile.

In summing up territoriality and ground displays, the easy course would be to say, and not without justification, that the Hudsonian Godwit is non-territorial, that intraspecific conflict over territory is lacking, and that ground displays are minimal. However, I cannot believe that this is quite true. Most shorebirds, and particularly tundra-nesting species, are territorial. The male Black-tailed Godwit (*L. limosa*) is highly territorial, engages in prolonged and rather severe boundary disputes with its neighbors, and has elaborate ground displays to which the female responds in lesser degree (Huxley and Montague, 1926; Lind, 1961; Haverschmidt, 1963). A particularly puzzling aspect of Hudsonian Godwit behavior is the timing of the peak of flight display: not early in the season as a preliminary and accompaniment of pair formation, site selection, and nest-building, as in other birds generally and the Black-tailed Godwit particularly; but after the eggs are laid and incubation is in progress. Another disturbing point is that the nests of *L. limosa* and *haemastica* are identical in shape and dimensions; if one is formed during a somewhat prolonged scrape ceremony, it is only logical to suppose that the other has the same origin. So why did we not see it?

Of the possible reasons, I discount failure of observation. We had godwits too constantly in sight during early June for any common routine to escape notice, especially routines we were expecting. Conceivably, the season was atypical as to weather, but there is no reason to think so. Another explanation, and perhaps the likeliest one, is that we have here a classic example of adaptation to the requirements of a long migration and a short harsh summer. In average terms, the Black-tailed Godwit occupies its European nesting grounds in early March and lays eggs from about 10 April to 25 May (Lind, 1961). The Hudsonian Godwit, on the contrary, must complete a clutch and be incubating within two weeks of arrival or successful rearing of the young is in doubt. In other words, some Hudsonian Godwits complete the whole nesting cycle and are gone in a shorter time than it takes some Black-tailed Godwits to lay eggs. To accomplish this, is it possible that *L. haemastica* has effected a very marked shortening of some courtship routines and delayed the peak of song-flight to a time when its food requirements are more easily met? The need and indeed the opportunity for further study are quite obvious.

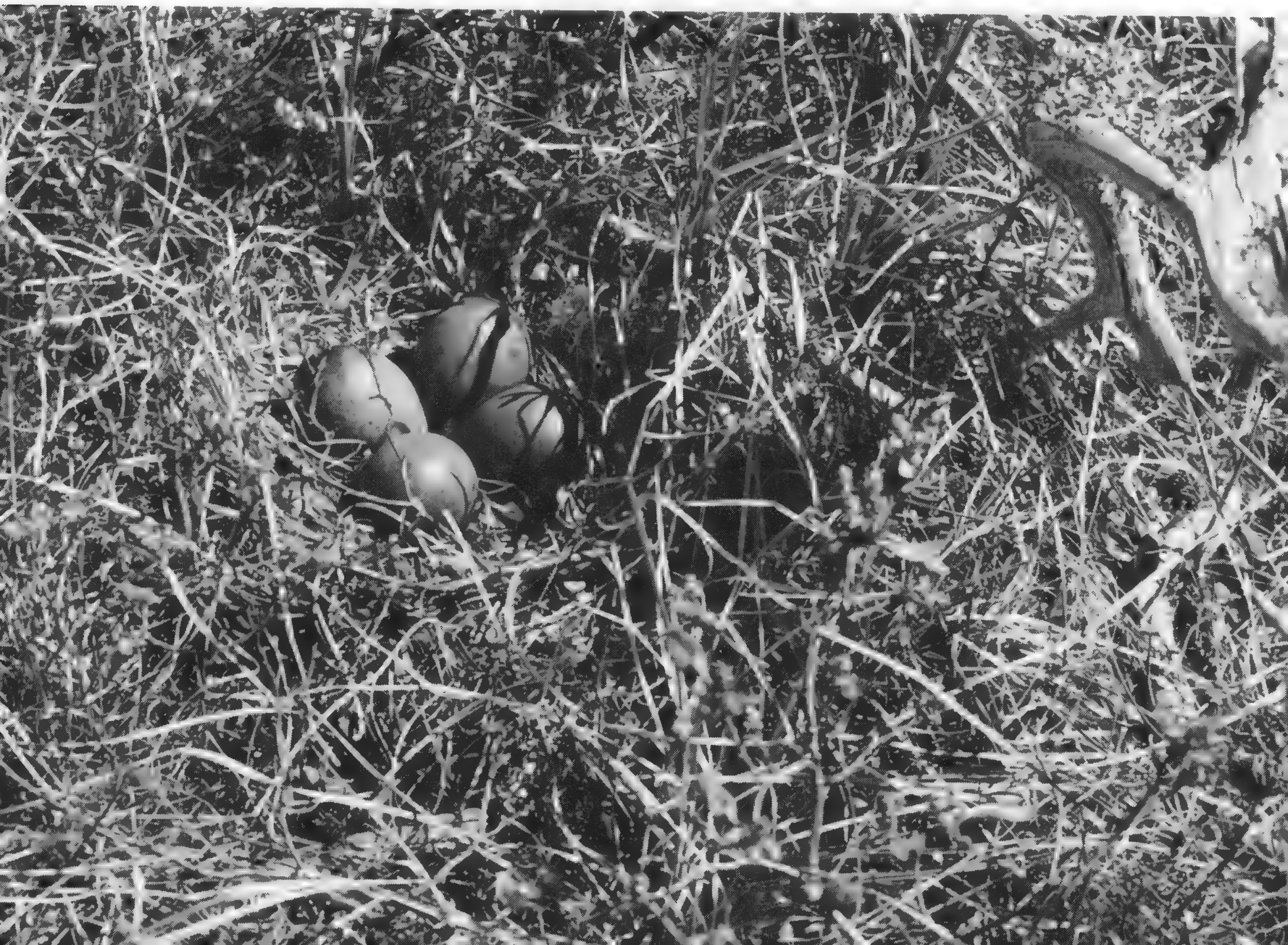
Nest, Eggs, and Incubation

The nests of the Hudsonian Godwit, even in habitat where the bird is numerous, are extremely hard to find, because of the dissociation between nest and feeding grounds and the furtive nature of nest-relief. In all our watching, we were never forewarned of a change-over by the actions of a relieving bird, nor did we hear any special calling to indicate that a change was taking place. Without these clues, so often supplied in other species, nest-hunting comes down to the methodical beating of a favorable area. This searching reveals two other traits of the godwit: if the off-duty males show themselves to the intruder at all, they either continue to feed unconcernedly in the marsh, or sit quietly on the tops of spruce trees, occasionally calling *whee'-wit* but never with enough variation in excitement to indicate that the search is turning warmer or cooler; the females, meanwhile, sit so tight that a beater must come within two or three feet of one to be sure of kicking her off, and within 10 or so to start even the least tenacious. This behavior is unusual among tundra-nesting shorebirds, many of which, presumably warned by the calls of their neighbors, rise well ahead of an intruder and fly to meet him. The difficulty in locating nests is the second major reason for the long delay in working out the breeding range and status of the Hudsonian Godwit.

A typical nest (Figure 5) is a saucer-shaped depression, about five inches across, in or under the edge of a prostrate dwarf birch on the dry top of a hummock in sedge marsh. Depending partly on the season, the surrounding marsh may be several inches deep in standing water, or no more than damp under pressure. One nest in four or five may be in a tussock of grass or sedge, and, occasionally, a nest is placed under or among small willow bushes. A nest in an otherwise open situation is sometimes beside, or near, the bleached pole of a long-fallen spruce tree or some similar object which may serve as a marker; this is the same tendency which appears in Greater and Lesser Yellowlegs (Randall *in* Bannerman, 1961) and the Greenshank of Eurasia (Nethersole-Thompson, 1951). The cover at the nest-site, whether shrubby birch or grass, is usually at least five or six inches high and thick enough to conceal the sitting bird until she is almost underfoot; the top, however, is nearly always open. The scrape is nicely formed and smoothly worked, often with no lining except a few dead birch or willow leaves which have more the look of being blown in than placed there, occasionally with a more substantial lining of grass and leaves. An occupied nest in 1964 had one side formed by a prostrate branch of birch; directly on the other side of the branch, and slightly lower, was another nest-scrape identical in size and depth. Since its bottom was covered with dead leaves and its sides showed no evidence of recent shaping, this scrape appeared to be a nest of the previous year and was possible evidence of site tenacity.

Like other northern shorebirds, the Hudsonian Godwit so consistently lays four eggs in a clutch that a lesser number usually indicates some post-

Figure 5. The nest and eggs of the Hudsonian Godwit at the site shown in Figure 2. Note in the foreground the stems and opening buds of dwarf birch.



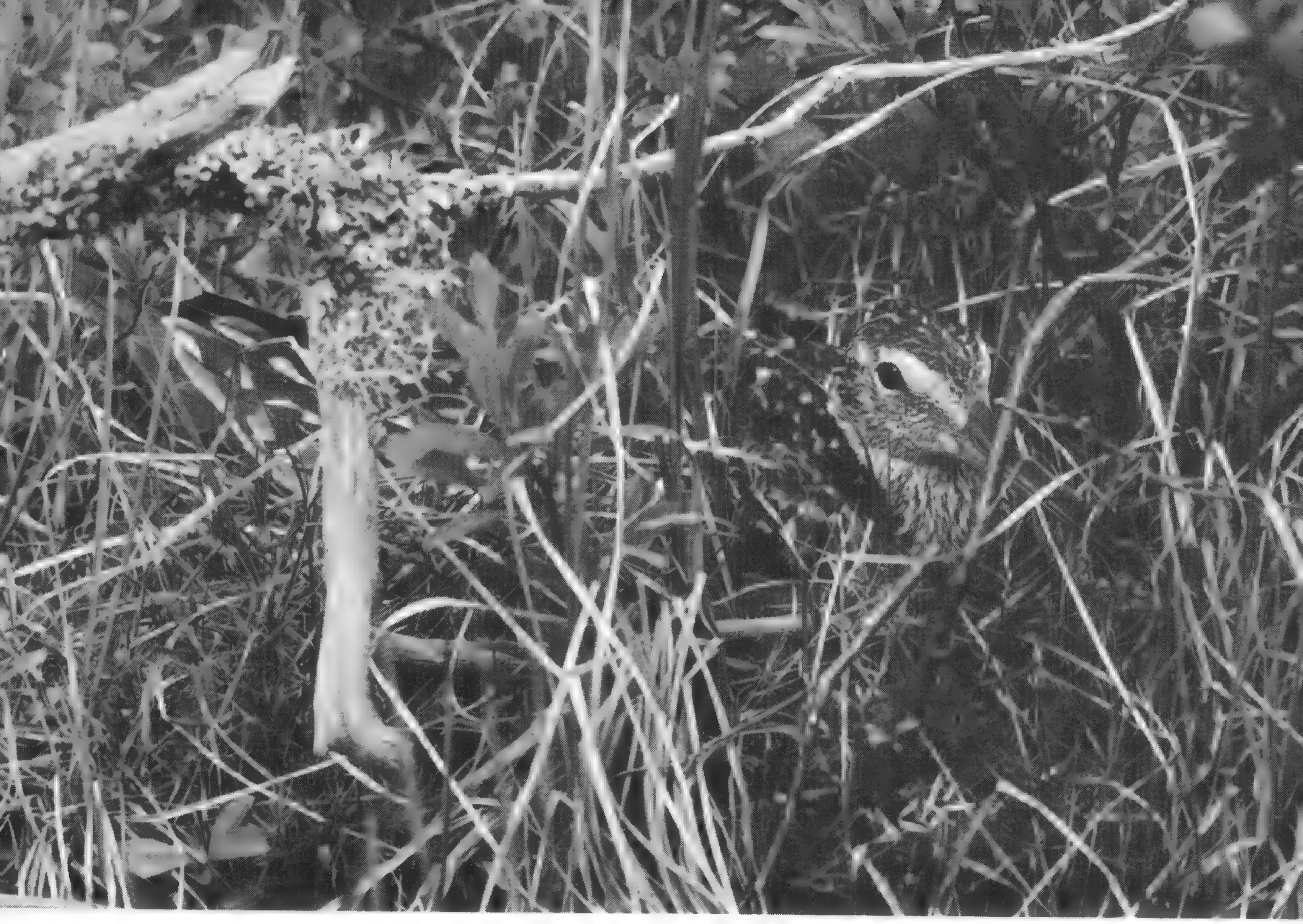


Figure 6. Female godwit, at the same site in Figures 2 and 5, sitting on pipped eggs, 5 July 1962. Note her relaxed posture and disposition of her bill, also the thick cover of dwarf birch and willow recently leaved out.

laying loss. No set of more than four eggs has been reported. Bent (1927) supplies a critical description of color and markings, based on five sets, and gives the average measurements of 27 eggs as 55.2 by 38.1 millimeters; his extremes are 60.6 and 51.0 mm in length, 41.2 and 35 mm in width. The average of 22 additional eggs from Churchill is 55.8 by 36.3 mm, with all extremes falling inside Bent's limits. To the uncritical eye, the eggs are somewhat darker and more olive- or greenish-brown than those of other Churchill shorebirds, and the markings less bold; they much resemble a common type of gull egg.

A female godwit returning to a nest habitually alights a short distance away and approaches on foot; she first settles on the nest lightly, with tail raised, neck extended straight up, and bill vertically down while she turns and arranges the eggs; this done, she relaxes into the normal incubating position, rather flattened out, the tail low, the neck comfortably flexed, the head partly raised to watch the surroundings, the long bill straight ahead and often rested on twigs or grasses beside the scrape (Figure 6). At rather long intervals she shuffles the eggs, turns herself a bit, picks up leaves and drops them again, even jabs at flies, as did a bird which Jehl was filming. On the whole, she is a quiet sitter. When any disturbance breaks out in the neighborhood, she raises her head higher to watch; if it comes nearer, she slowly flattens herself to the limit, extends her neck full length on the ground with bill thrust into the shrubbery, and, except for her eyes, never moves again until the danger has passed or is too close to ignore.

Nest-reliefs follow a regular pattern of female on the nest during the day, male on at night. Jehl made many checks of five nests during the 1965 season: his notes show the female incubating from about 7:00 AM to late afternoon or early evening, the male on the nest sometimes as early as 6:30 PM, and invariably by 9:00 PM. A pair which I watched in 1962 habitually changed places between 3:00 and 4:30 in the afternoon. From the frequency of pursuit-flights at about that time of day, I suspected other females were also being relieved. We have no direct observations of what takes place at a nest during relief. If there is a ceremony, as in the Black-tailed Godwit (Haverschmidt, 1963), it must be abbreviated for the elapsed time is only a few minutes.

During the incubation period there are progressive changes in frequency of display flights and in several other behavioral routines. In 1962, song-flights reached a peak from 27 to 30 June and then gradually diminished until the last was heard on 10 July. Pursuit-flights also peaked in the last week of June and the first few days of July, not only in frequency but also in the number of birds involved. Some questions thus raised can only be answered by extensive color-marking. Since all the females with eggs were presumably incubating during the day, the loose groups of godwits feeding in the tundra pools were predominantly males—by counts at different times, a sex-ratio of 8 or 9 to 1. As a result, if one of the few females not on eggs happened to initiate a pursuit-flight by the nearest male, the two were quickly joined by several other males, sometimes more; and as the first of the joining males dropped out, others rose in like proportion. Then, as the afternoons wore on and the sitting females began to come from their nests, more chases were set off, but the proportion of males declined because one by one the latter were taking over the duties of incubation.

When I first saw these multiple pursuit-flights, I did not fully realize what was happening. It came into focus rather quickly one afternoon about 3:30 PM when I was watching three birds—male and female near each other, a single male close by. A pursuit-flight started, and the odd bird at once took wing to join the other two, but within 300 yards veered off, went directly to a part of the meadow where we had found a set of eggs, and pitched very close to the nest-site. Within minutes a godwit rose from the same place, came towards me, lit within 30 yards in a pool, and immediately began to bathe. It was a female, obviously just relieved by the erstwhile flight-chasing male, a fact which I soon verified by going to the nest and finding a male on. From the foregoing observations, and others, I have an impression that pursuit-flights, whatever their original function, are somewhat less important in pair formation and maintenance than as social exercises in headlong twisting flight.

About 20 June, godwits begin to show the increasing solicitude for nest and eggs which presently culminates in "guarding." The volume of protest-calling, or scolding, increases steadily, and with it the flight-form, peculiar to this season of the year, in which the wings are held in downward arcs, always below the horizontal, and flickered quickly and continuously at their tips. Godwits invariably fly this way when circling an intruder, whether fox, bear, or man, and only resume normal flight, with strong deep strokes, when mobbing jaegers and other birds or in traveling some distance across the tundra. I find no published references to fluttering flight in other shorebirds, including other godwits, but at least some of them use it in one of several versions—e.g., Whimbrels in the nesting season flicker their wings, but about equally above and below the horizontal line of the back.

The growing parental solicitude of the adult godwits is now evident in flushing behavior. A female forced from her nest in the first week of incubation is inclined to take it calmly—she comes off with a rush, alights within 20 yards or so, and calls *whit, whee′-wit* in no more than moderate excitement. Her mate may appear within a couple of minutes, and the two birds circle about, occasionally alighting on the ground or atop nearby trees, the female continuing to call pretty steadily, the male occasionally. For contrast, flush the same bird on the day her first egg pips. She explodes from the nest as before, but whirls in a sharp turn not more than a dozen feet away and comes straight for your head with a harsh, heron-like squawk from which you instinctively recoil. She is not likely to strike you, but will come close enough to be caught by hand—except, of course, that you are temporarily paralyzed by the unexpectedness of the attack. A moment later she is shrieking *whit, whit, whee′-wit, whit, whee′-wit* at the top of her voice, and reinforcements are pouring in from all directions. Within a minute or two there are from six to 10 godwits circling your head in noisy protest, and with them, contingents of Whimbrels, Lesser Yellowlegs, Short-billed Dowitchers, and Stilt Sandpipers, each species taking part according to its own nature. The yellowlegs are the most excited, flying from one treetop to the next and scolding vociferously; the Whimbrels noisy but more aloof, perching on trees at a greater distance; the Stilts inclined to stay on wing, circling close in and calling a bit, their voices pitched so low as to count for nothing in the general uproar; and the dowitchers, quietest of all, sitting about on the tops of bushes and small trees, just watching. The extra godwits are usually males and, as noted for pursuit-flights, their interest in the disturbance varies from one bird to the next. They presently begin to drift away, the other birds disperse, and in the course of five minutes only the resident pair, or perhaps only the female, is left to protest your presence.

The incubation period of the Hudsonian Godwit, on the basis of three explicit records, is 22-23 days. The clutch watched by Miss Ellis in 1947 was completed on 16 June; all eggs were pipped on 7 July; and all hatched on the morning of 8 July, an elapsed period of 22-plus days. Dr. Allen's nest in 1954 had the fourth egg laid 10 June and the chicks hatching on the evening of 2 July—again 22-plus days. In 1965, Jehl made the most precise observations yet available: at 4:20 AM on 24 June the male was covering three eggs and had presumably been incubating since the previous afternoon; the fourth egg was added later the same morning; and all four hatched on 17 July. He fixes the period in this instance at 23.5 days ±5 hours. Incidentally, there is other evidence that incubation probably begins with the laying of the third egg.

From such data as we have, it appears that godwit nests are not particularly vulnerable to either predation or the exigencies of weather. However, this statement is tentative. Certainly a late snowstorm at Churchill often does great damage and godwits cannot wholly escape. On the other hand, godwit nests are in thicker cover than those of many species, the birds sit much more tenaciously, and in general the species is robust to a marked degree. In some years, the whole hatch of godwits seems to come off within a few days, and the spread of the most irregular hatches seems to be not more than two weeks. A calculation from 10 known nests shows 30 chicks hatched from 36 eggs—a success of 83 per cent.

I close this section with an odd note about the female: having sat on the eggs during the day, when the sun's rays reach her most directly through the clear atmosphere of the Subarctic, the feathers of her back are noticeably more bleached and faded at the end of incubation than those of her night-sitting mate.

Downy Young

From a search of the literature and inquiries addressed to the larger museums of the United States, Canada, and Great Britain, it appears that no Hudsonian Godwit chick in the downy plumage had been collected prior to 1962; the black-and-white photographs published by Miss Ellis (1948) and Congdon (1952) constitute the only information. Since 1962, I have deposited a small graded series, aged eight hours to about 19 days, in the Museum of Comparative Zoology at Cambridge, Massachusetts, and supplied representative specimens to the Royal Ontario Museum and the National Museum of Canada. Jehl has also taken specimens of various ages, and some of these I have seen at the University of Michigan Museum of Zoology.

To supplement the excellent likeness of a day-old chick (see Frontispiece) which Dr. Sutton has painted from specimens, photographs, and my field notes, I offer the following description:

> Ground color light buffy-gray to buffy-brown, tending to browner on lower neck, sides of breast, and thighs, to paler on head and mid-back, and to grayish-white on upper throat and belly; dorsal markings, a broken pattern of brownish-black stripes and splotches not sharply defined; on head, a very narrow black line from base of bill to anterior corner of eye on each side and another up central line of forehead; a brownish-black crown-patch not well defined in front but sharper behind, and, extending downward from its rear edge, three short stripes of same color, one centrally down nape, the other two symmetrically on either side of head between the central stripe and the auricular region; bill black or blackish with base of lower mandible shading to dull purple-pink in life, pale yellow-horn immediately after death; eye dark; legs and feet dark slate with bluish tinge. At hatching, egg-teeth on both upper and lower mandibles which drop off as soon as bill is dry.

The three occipital stripes of the Hudsonian Godwit chick are diagnostic with respect to any other Churchill shorebird, and, on comparison with the downy young of the other godwit species, prove to be so for the genus. Otherwise, the comparison reveals some rather marked variations in ground color, both intra- and interspecific, with *L. haemastica* the grayest of the lot. There is also the interesting fact that godwit chicks are mottled rather than spangled on the dorsal surface, thus falling into the group which includes curlews, yellowlegs, and willets. Since the implications are chiefly taxonomic. further discussion is deferred to another paper.

Growing Period

The time of rapid growth in the Hudsonian Godwit chick, from hatching to full feathering and near-adult size, is approximately 30 days. The highlights of the period are the quick increase of strength and mobility in the first 48 hours, the guarding routines of the attendant parents, the maintenance activities of the growing young bird, and the sequential development of its feet and legs, its bill, and its wings. The first and last of these may be studied from live birds in the hand and during the preparation of specimens. The second lends itself to simple observation. Collecting data on the third is a problem: most of the sedge marsh at Churchill is fairly open from above but dense from the side, and the tundra has few vantage points which afford a view of what godwits are doing on the ground after the third week in June.

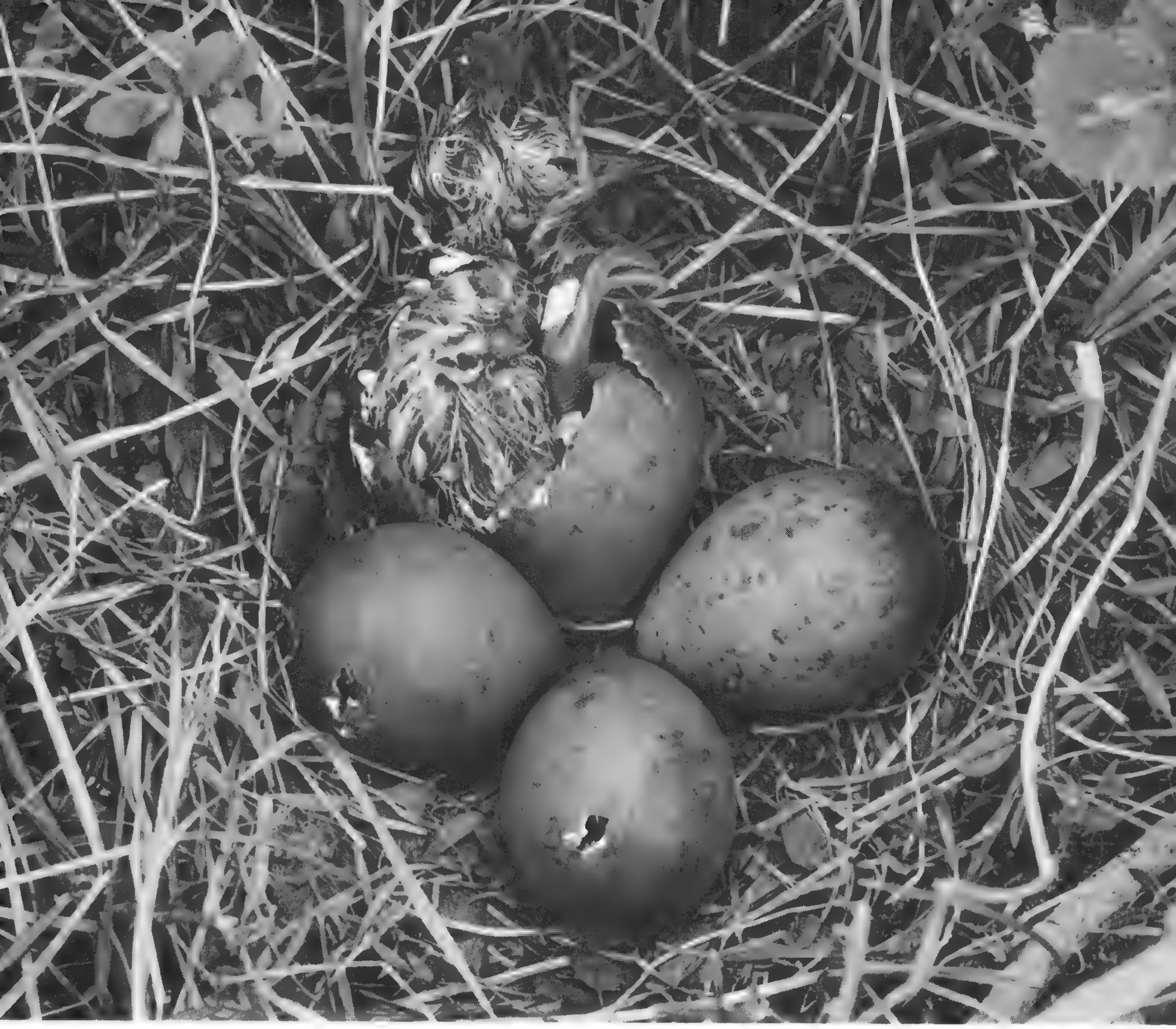


Figure 7. First Hudsonian Godwit chick pushing from egg, Churchill, 10:30 AM, 6 July 1962. Already its short, firm bill and one large foot and leg can be clearly seen. The nest is well lined with leaves and grass.

Four or five times only, I came across young birds close to a raised roadway, and was able to watch them from my car without disturbance. For the other aspects of the growth period, I have notes on three nests in which chicks were emerging from eggs when the incubating adult was put off, saw guarding behavior on scores of different occasions, and closely examined about 30 older chicks whose age was known or could be estimated to a day or so. On the whole, this material falls short of being conclusive, but still serves to outline some interesting areas for further study—and not only of godwits, but of other tundra-nesting shorebirds, because published references to this part of the breeding cycle are nearly lacking.

If appearance may be taken at face value, a godwit chick, at the moment of kicking itself free from the egg, is exhausted by its labors of the preceding 24-36 hours in breaking through the shell (Figure 7); for a few minutes it lies on its side, wet and bedraggled, its eyes closed, before making the first feeble attempts to right itself. Picked up at this point and examined gently, it already shows disparities in the relative size of its several parts: the bill about half an inch long and already quite firm, as it would have to be for breaking out; the forward half of the body almost wholly undeveloped, with the wings represented by tiny flaps of soft skin on either side; the belly relatively

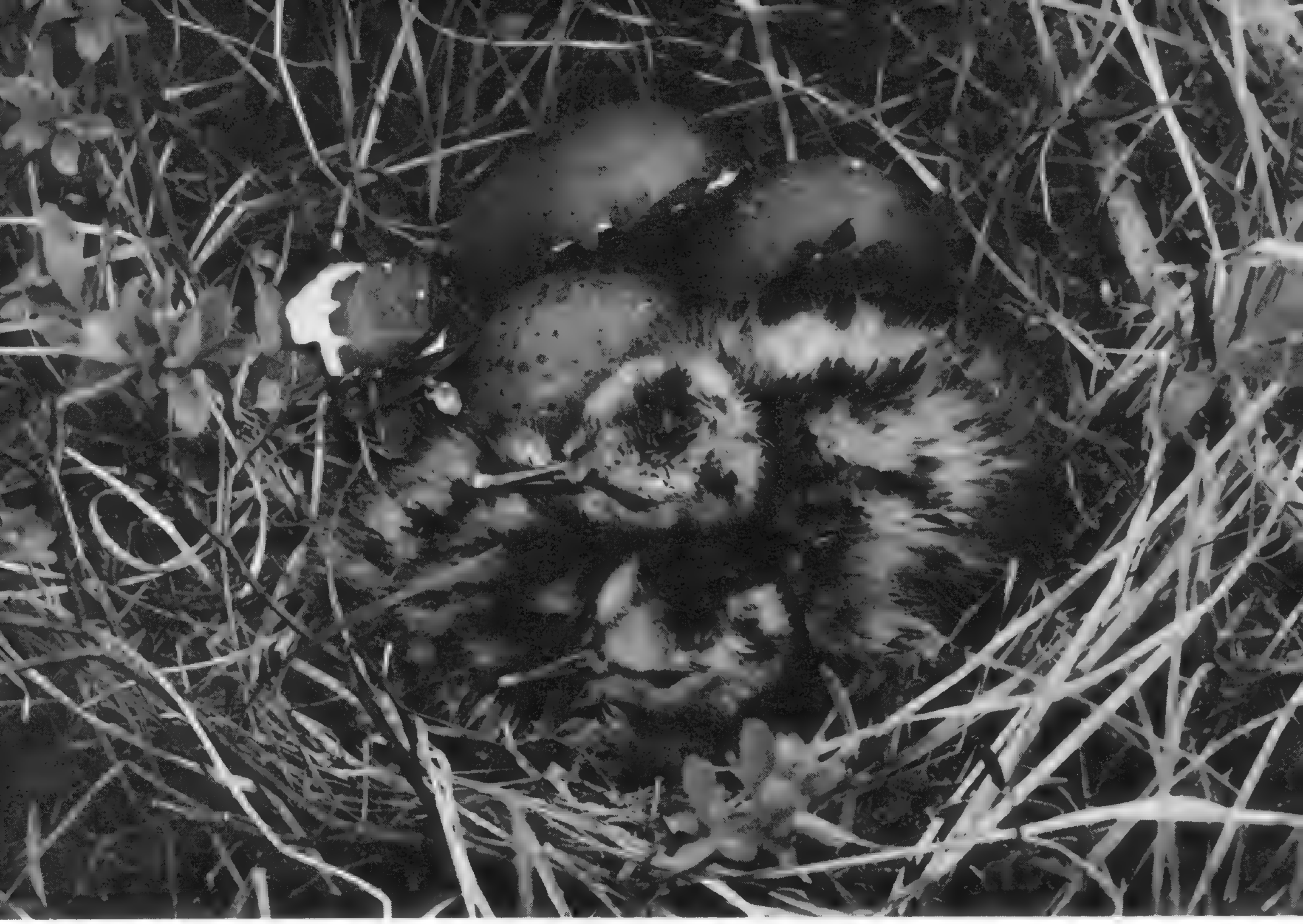
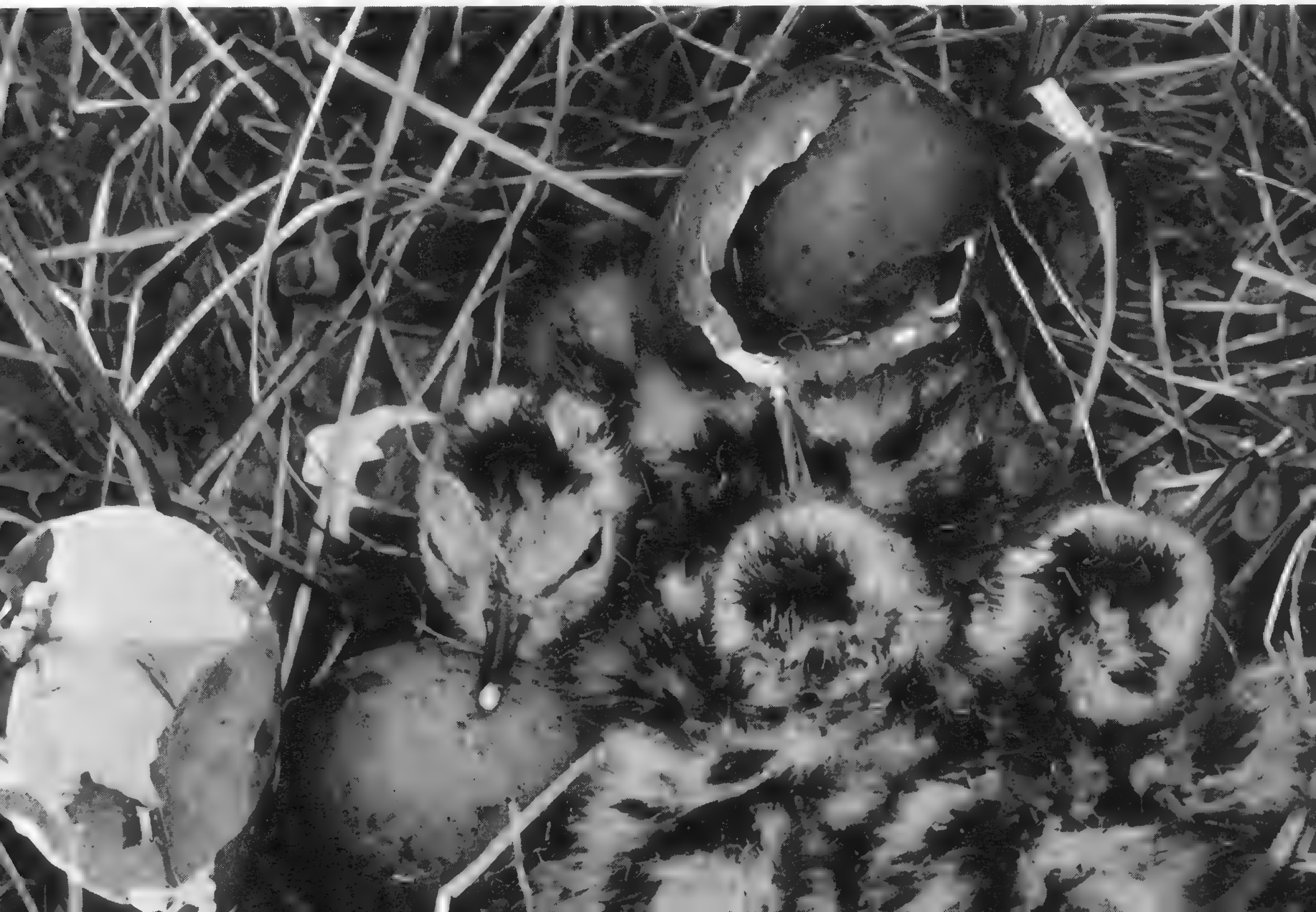


Figure 8 *(above)*. The same nest as in Figure 7. Three Hudsonian Godwit chicks (one not visible) hatched and dry at 4:15 PM, 6 July 1962. The fourth egg hatched during the following night and the whole family was 200 yards away in midmorning, 7 July.

Figure 9 *(below)*. The same nest at same time as in above figure. The chick at right, at less than six hours from hatching, has already lost the egg-tooth on its upper mandible; the two later-hatched chicks still retain their egg-teeth. Note the large asymmetrical openings in the egg-shells.



large, with a scarcely healed scar where the egg yolk has recently been enfolded within the body cavity; and the legs and feet, still soft, so remarkably large that they seem to be half of the bird.

Two hours later, an adult having been allowed to brood in the meantime, the same chick is a bright-eyed ball of fluffy down so lively that it may be already out of the nest and hiding in the vegetation nearby (Figures 8 and 9). Again picked up and examined, its legs and feet are found to be still very large, but now dry, somewhat hardened, and much stronger; the middle toe is nearly as long, and the span of the opened foot nearly as great, as in the average adult. When a band-gauge is applied to the tarsus, the minimum diameter is four millimeters, slightly *larger* than the corresponding measurement of the hard bony adult tarsus; the joint at the distal end is sufficiently swollen so that the chick may be banded at once without risk of loss, which is true of few other birds.

The length of time spent in the nest varies with the interval between hatching of first and last chick, but this is frequently, perhaps usually, rather short. In one nest the first chick was just out at 10:30 AM, the second and third out and dry by 4:15 PM. In another, the first chick was dry and the second just out at 5:30 PM, the second dry and the third out at 7:15 PM, the fourth partly out at 8:30 PM. In still another, hatching began in midafternoon and was completed by 7:30 PM.

From these data, and observations on chicks already away from the nest in midday, I suspect that most broods hatch between noon and midnight, and leave the nest before eight or nine o'clock the next morning, the several members of each brood being then 10-18 hours from the egg. As they leave, the chicks are capable of threading their ways through vegetation and across rough ground with considerable speed, swim readily the small pools and runs which lie among the sedges, and are adept in hiding or freezing at a warning call from one of the parents.

By the end of the second day abroad—i.e., at about 48 hours from hatching—they are much faster afoot, show no hesitation in swimming broad, rough waters when pressed, and are brooded very little unless the weather is severe. Most remarkable of all, to the observer not acquainted with shorebird ways, is the fact that they find and catch their own food, chiefly insects at this stage, and have done so from the very first sallies outside the nest. The parent birds "guard" assiduously, and I assume — without direct evidence — that one of them broods at night until the young are partly feathered, but there is no indication that they play any other part in rearing the chicks.

The guarding routine is interesting for a further division of duties between the two parent birds: the female usually sits rather passively on the top of the tallest nearby tree, keeping a watchful eye on the neighborhood, while the male engages himself in active leadership of the chicks, either away from danger or in the direction toward which the family is moving. Three cases, condensed from my field notes, will show the general pattern of guarding, and how consistently the old birds maintain their separate roles.

> *7 July 1962.* At 5:30 PM, pair of godwits near causeway, male sitting quietly on top of small larch, female probing in edge of grassy pool; neither bird took alarm as we drew up and stopped abreast of them. We suspected chicks, and in a matter of minutes saw two, about 48 hours old, running about on a raised mossy area between the two adult birds. Rushed them and caught one but missed the other, which hid. Both adults

around my head in a fury. Withdrew to car and in 10 minutes, as old birds quieted down, saw second chick run toward male. Rushed it again, and found it lying flat behind lump of peat, facing toward road. Back to car, banded chicks, and released them. The parent birds had been shrieking around car—*whit, whit, whee′-wit, whee′-wit*—but as soon as chicks started down bank, male flew to mound about 60 feet out in marsh and began to call *whit, whit, whit* in softer tones, no longer excited or hurried; chicks made off quickly in his direction, and in no more than a minute disappeared beyond him. Female continued to circle car, lighting briefly from time to time on road or in marsh nearby, until we left.

13 July 1962. A mile north of Back Hill at 11:30 AM, pair of godwits ahead of us, male standing in road, female feeding in small grassy marsh as we drove up, but immediately rising to light on dead spruce tree. Both called *whit, whee′-wit* as we stopped, and I had an instant suspicion we had surprised male in act of leading a brood across the road toward the Hudson Bay shore, half a mile away. He flew from road, lit beyond female, and soon afterward one chick, followed by another, ran up slope of a dry ridge and over the top toward him. Obvious now that his calls were leading them away from us while female watched from treetop. In next few minutes he moved several times, always a little farther away. At length he flew down behind another low ridge and was out of sight for several minutes. Threw door open and ran toward him: female off her tree at once, shrieking, and male rose before I had taken 20 strides. As I crossed the ridge, saw that he had jumped from small sedge marsh; watched the slope beyond it, but no chick moved. Searched the rather sparse cover methodically, while both old birds scolded close at hand, alternately on wing and from hummocks and small trees. After long hunt, suddenly realized female was watching more quietly from a tree, while male had moved away across the barren westward. He certainly had the chicks with him, and further search seemed useless.

15 July 1964. Toward Farnworth Lake in late forenoon and came across pair of godwits in narrow strip of barren between road and sizable lake to the east. Birds very excited as we drove up and obviously had chicks nearby. Soon sensed that male was working northeastward along shore of lake, probably guiding them away. As we stood on bank overlooking lake, two of them swam out from a sedge-covered point of marsh to our left and headed diagonally across in front of us, the wind at their backs, toward farther shore. Went around and intercepted them soon after they landed—about three days old, not wet from a swim of 300-400 feet, nor yet tired, because one almost got away before I could catch the other. Carried them back to starting point, put them in netting bag, and laid bag on open moss with object of bringing parent birds within short camera range. Successful in this, and soon found that we had unwittingly set up small experiment in guarding behavior as well. For few minutes both birds scolded vociferously, circling around and lighting on nearby stubs, but presently, and at short intervals thereafter, male broke away, flew up west lakeshore, and lit on tops of spruces where he gave the softer *whit, whit* calls which guide chicks. Supposed at first he was calling to the pair confined in bag, but as he went farther away each time, it became evident he was leading away the remainder of his brood. During one of his absences, female began to perch on top of 20-foot live spruce a gunshot away from

> us, much less excited than at first, and presently remained there even when he returned to shriek at us from a stub within 16 feet of where we sat. In course of 15 minutes his successive moves had carried him 350 yards up the lakeshore, and now he waited there a considerably longer time before coming back to scold us. As he left us this time, he went *across* the lake and lit atop a dead stub on the eastern shore a full quarter-mile away. Plainly enough, during his prolonged wait just preceding, the remaining chicks had also swum the lake, and unlike the first two, by quartering into the wind. They presumably remained near their landing place, because male used same perch for next hour, coming back at about five-minute intervals to scold us. As result of these many returns, we discovered, quite by accident, that they followed a pattern not previously suspected. On his distant stub, we could recognize him by his posture, subtly different from either Whimbrel or Lesser Yellowlegs, and events proved he was equally aware of us. If he had been there a few minutes, and I made the slightest move of hand or arm, he was off his perch in an instant and speeding up the lake toward us, calling continuously in harsh tones; he invariably passed about 20 yards out over the water, swung up behind us into the wind, and came back by on flickering down-curved wings to alight on one certain tree. Having then scolded us thoroughly for half a minute or so, he started away again and went straight back to his departure point. But here was the interesting detail: from the time he left us, I could stand up, wave my arms, walk around—nothing turned him or caused him to come back until he had reached his stub and perched there quietly for a couple of minutes. It seemed that he required a short period to recharge his energies. When the time had passed, a wave of my arm triggered the whole cycle again, but until then he paid no attention. To this extent, at least, his response to "chicks in danger" was quite mechanical. As for the female during this hour and more, she never left the vicinity, kept up an intermittent and only moderately excited *whit, whit, whee'-wit* from her treetop, occasionally joined the male in alighting on stubs very close to us, even lit two or three times, briefly, on the ground beside the captive chicks, but on the whole was relatively placid. Of the two chicks, one tried incessantly to get out of the bag, the other lay quiet. They sometimes called—a very thin, high-pitched *peep, peep,* barely audible to me at 10 feet. For the most part the female gave no indication of hearing them, but once only, when both were peeping, she left her tree in some excitement, hovered over them a moment, and finally lit for an instant beside them.

Summing up these notes on guarding, the male stays near the chicks except for periodic forays toward any source of trouble, at which times he is the more aggressive; the female maintains a wider guard in time of danger, perching on higher trees, warning of trouble before it is near, and keeping contact with the danger as the male moves the chicks away. There is, however, one point at which the roles may be reversed: if it comes to a crisis, as when a chick is about to be caught, the female is more likely than the male to actually close with the intruder, at the same time giving the loud rasping squawk which is so disconcerting.

Two more observations will complete this description of guarding behavior during the first week or 10 days after the chicks hatch. It is already evident that a godwit family covers considerable ground from the very beginning, and although extensive color-marking of adults and banding of chicks will be necessary to prove the point, I suspect the movement is not random, but directed toward the coast. The circumstantial evidence of this is twofold: by mid-July there are many broods north of that part of the Twin Lakes road which parallels the shore, where there were none before; and soon afterward, the number of guarding pairs in the southern edge of the nesting belt begins a progressive decline somewhat greater than might be accounted for by loss of broods to predation.

The other fact, and a curious one, is that a female excited by some threat to her brood rather frequently flies above the intruder with the same owl-like flapping which was earlier used by the male at the climax of his song-flight. She waves her wings with exaggerated slowness through the narrow arc between 30° and 60° above the horizontal, and what purpose is served does not appear.

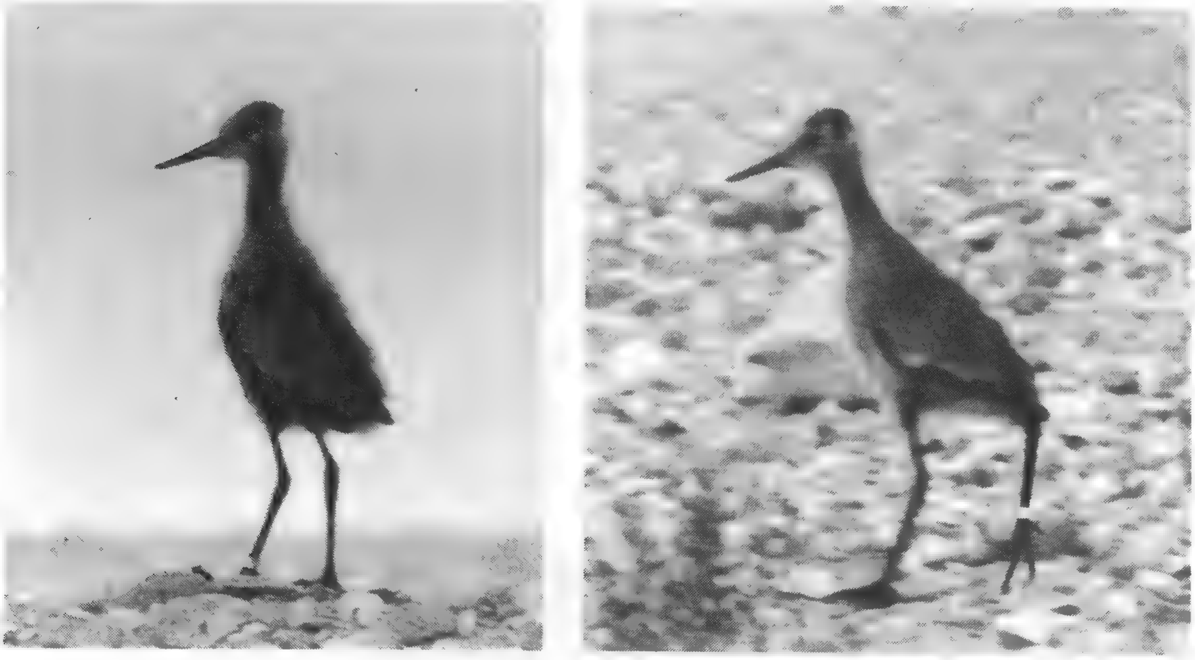


Figure 10. Two views of a young Hudsonian Godwit 17–18 days old, Churchill, 22 July 1964, show its crane-like posture and appearance while its tail and bill are still short.

Of the latter part of the rearing season, what little can be learned in watching is by inference from the actions of the guarding adults. They advertise the general location of the chicks, but the latter are soon so long-legged and strong, so well able to cover the rough ground at a fast clip, that for the most part they keep far ahead of trouble. By riding the roads in a car, it is sometimes possible to surprise a brood in a situation where they freeze or hesitate for the few moments needed to stop, tumble out, and gain position to head them off, but not all can be caught. Much less often, one or two can be seen feeding in some slight depression—dashing about with great agility in pursuit of flying insects, or probing the surface litter and the edges of the pools for larvae and small mollusks. At two and three weeks of age they bear a passing resemblance to miniature cranes which the adults never have—the long legs, the short tail, the bill, are all in about the right proportion, and the upright carriage of head and neck completes the illusion (see Figure 10).

While a full account of differential growth of feet and legs, bill, and wings in the young Hudsonian Godwit must wait on more extensive investigation, its general course is outlined by data in hand and is too significant to wholly pass by. In kind, the problems involved are those of any bird growing from egg to adult, but the godwit must accomplish a greater transformation than most birds, in circumstances which are quite possibly unique.

One way of arriving at full appreciation of this fact is to compare the godwit with its summer neighbor on the tundra, the Willow Ptarmigan. The ptarmigan is a generalized sort of bird, with no unusual development of bill, feet, or plumage; it subsists on buds, leaves, and berries, of which one or another is widely available throughout the year; and it is more or less sedentary, at most moving a short distance south of treeline in winter and by easy stages. A ptarmigan chick, as it comes from the egg, has bill and feet of about the same proportionate size as its parents, and its growth to adult size is essentially even and gradual.

The adult godwit, on the other hand, is a highly specialized bird: it has evolved long legs and, relatively speaking, a very long bill in order to exploit a sub-surface source of food which is not available to birds with short bills; and by some further quirk of evolution, which so far defies explanation, its present-day existence seems to depend upon its extraordinary migrations, which greatly increase energy requirements while reducing the time available to satisfy them. The godwit chick, issuing from the egg, must not only grow the bill, the legs, and the flight capability of its parents, but do so in considerably shorter time than the ptarmigan chick. The Subarctic days are long, insect food abundant, and on this base the two species build their separate patterns of development, the one rather evenly unselective, the other highly differential.

In the young godwit, growth is directed successively into those parts of its body which it will use next. The chick starts with the advantage of coming from an egg which is large in proportion to size of adult, allowing for greater prehatching development. Its first need is for big feet and strong legs to carry it about in a difficult environment; accordingly, its feet (length of middle toe and span of spread foot) are approximately 90 per cent of adult size and in less than a week are as large as they will ever be; its tarsus is already fully developed in diameter (and probably in strength too) but is only about 50 per cent of adult length. Next in order, the chick will use its bill, but since a short bill is more easily disposed in the egg and is well suited to dabbing at surface food, length at hatching is only 20 per cent of average adult length, its further growth delayed. Third on the priority list is a large digestive system to turn gathered food into more energy; at hatching, the abdomen is disproportionately large and continues to grow fast during the next three weeks. Fourth is a covering of body feathers for protection against an uncertain climate; the natal down suffices for a few days and within a week the first feathers can be detected emerging on the upper back and the sides of the breast. Last required, and therefore longest deferred, are the components of flight capability — wings and flight feathers, pectoral arch, and pectoral muscles. All are extremely undeveloped, almost rudimentary, at hatching.

The wings start first and grow steadily, with the tips of the outer primaries showing at about 60 hours and beginning to break their sheaths by the sixth day. The pectoral arch and muscles lag far behind, making only enough growth to support the growing wings until about the 18th day. At this point (see Figure 11) the bill is about half its final length, the legs approaching full length, the body feathers well out, the flight feathers more than half grown, the abdomen fully developed; rather suddenly the rate of growth in the forward half of the body increases. By the 28th day the young bird has much the same proportions as the adult, except that the bill will not reach full length for another month or so.

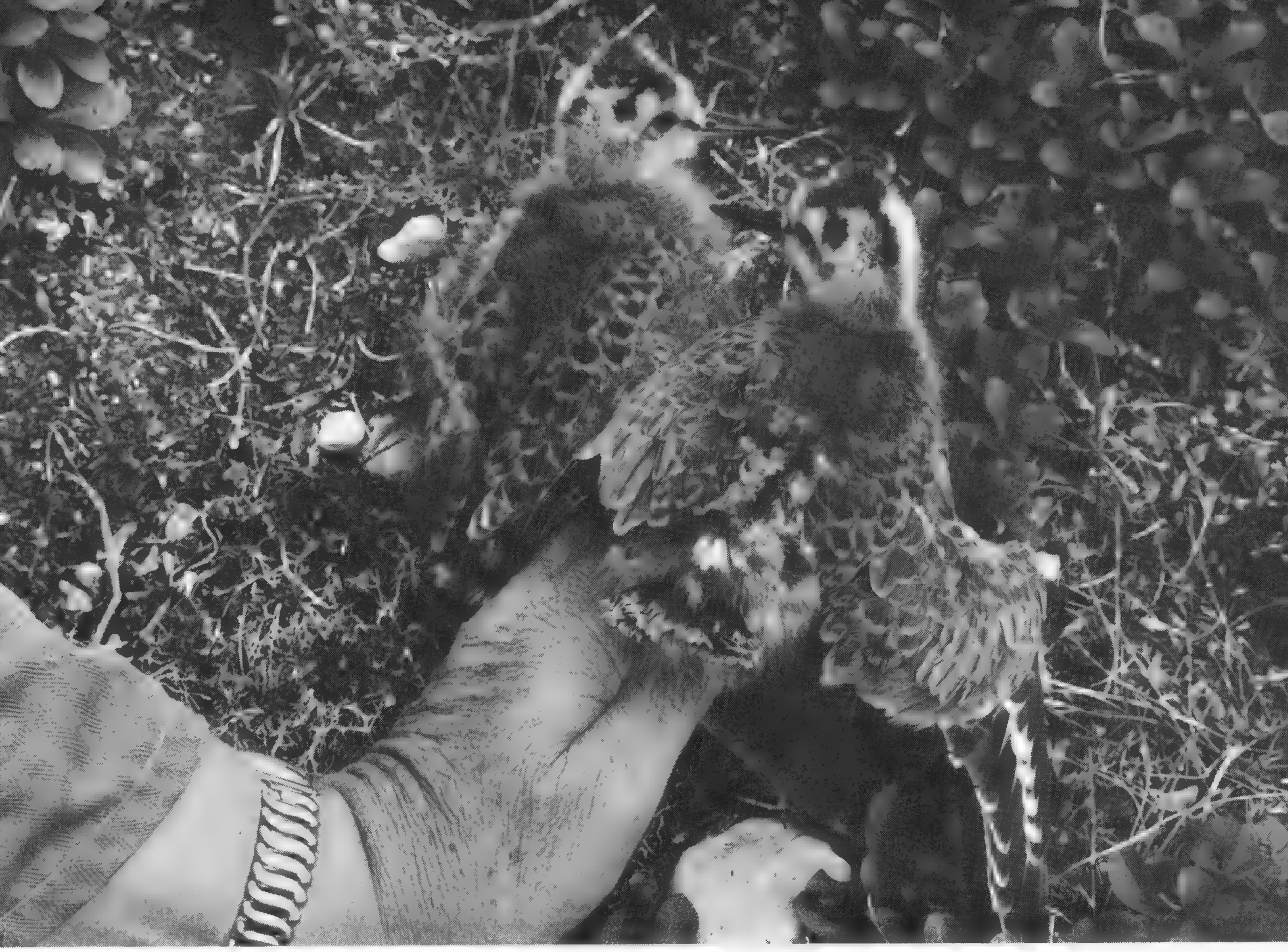


Figure 11. Sibling Hudsonian Godwit chicks 16–17 days old, Churchill, 25 July 1964. Their downy crown patterns persist. Though their wings are not yet strong, the wing feathers are nearly grown and show a distinctive color pattern.

The central fact of the growing period in the Hudsonian Godwit and, indeed, of its whole nesting cycle, is the extreme compression of one stage into another, the cutting of every corner to save time. Arctic shorebirds as a group have developed a pattern of fast growth beyond most birds; the godwit completes its cycle among the first and, all things considered, is probably outstripped by none.

Departure

The withdrawal of the adult Hudsonian Godwits from their nesting grounds is unobtrusive—so much so that most of the evidence is negative and again the sequence of events must be constructed by inference. In general, the pairs guarding chicks are numerous and noisy until about 20 July when their thinning out on the southern edge of the nesting strip first becomes apparent. Nearer the shore, the change is not obvious for a few more days, presumably because gaps are filled by family groups moving up from the south, but by 27 July even the coastal belt is noticeably quiet. Another three or four days and only an occasional belated pair can be found.

Several minor aspects of the withdrawal may be touched on briefly, beginning with a flurry of movement noted at the end of June in 1962. In the extensive marsh east of the Twin Lakes causeway, a number of small mixed flocks of godwits, Short-billed Dowitchers, and Stilt Sandpipers—from 15 to 55 in a flock—appeared suddenly on the 29th of the month, made themselves conspicuous for a few days by coursing about over the tundra whenever they were disturbed by Marsh Hawk or jaeger, and dropped from sight again by 3 July. Whether this was a significant gathering, and was made up of adults which had lost their eggs, or of nonbreeding subadults, remains for future determination.

The first passage of godwits from farther north was noted on 19 July 1962, a flock of 12, and on 18 July 1964, a flock of 20 seen by Jehl. In 1962 there were small flights during the late afternoons of 22 and 24 July, the largest flock running to 35. Without exception, these flocks came from the northwest across the corner of the Churchill bight, and went off southeast over the tundra on a course which would bring them to the Hudson Bay shore again some 12 to 15 miles south of Cape Churchill. Except for one small flock which lit on a sand bar for less than five minutes, these birds were flying very fast, at moderate height, and silently—in short, they acted like migrating birds from a distance, not like local birds taking their departure.

My sharp watch for local birds in the act of leaving their young in late July was unproductive. The only clues were an occasional single adult, very rarely a pair, flying north from the nesting country toward the bay shore during the last week of the month. Complementing this movement, a scattering of adults appeared on the shore flats after 20 July. When these birds were approached, they started up at some distance and showed traces of guarding behavior, circling toward me and calling *whit, whee′-wit,* but they lost interest almost at once, lit again on the flat, and resumed feeding. Single birds and twos or threes were most likely to react in this way; the larger the group, the more silent. Six of these adults were collected on 22 and 27 July; all showed brood-patches extensively filled in with replacement feathers still in sheath; their reproductive organs were largely but not wholly regressed. All were beginning the molt of body feathers, particularly on the underparts.

I spent the greater part of five days in 1964 watching these shore adults to see if any of them flew inland after feeding to resume guarding of chicks. None was seen to do so—at high water they rested on some elevated bar, as they do in migration. During the same days, I kept track of six or eight pairs still guarding on the tundra to see if one parent disappeared before the other. The females tended to become listless about their guarding duties a day or two before the males, but I turned up no case of a single guarding adult—either both were present or both had left. If they do not go together, it must be that the departure of one soon causes the other to follow.

The young birds I have left to the last, because there is literally nothing more to tell. By late July they are so well grown, so fast on their legs, so accomplished at keeping out of sight and ahead of danger that catching a glimpse of a single bird is almost impossible. When the adults no longer advertise the location of the young birds by guarding, the latter drop from sight completely until, a week or ten days later, they appear on the shore, fully feathered and flying. The nesting season is over.

Summary

Although the Hudsonian Godwit (*Limosa haemastica*) has long been considered a rare and decreasing bird, it is now known to be common in summer in parts of central and northwestern Subarctic Canada. In fall migration it passes down the west shores of Hudson Bay and James Bay in large flocks, and is not reported again in equal numbers until it reaches wintering grounds in southern Argentina and Chile. Following a summary of fall migration, known and speculative, this paper gives a descriptive account of nesting at Churchill, Manitoba. The nesting habitat is a relatively narrow strip of sedge and moss-lichen tundra lying in the northern edge of treeline, inland from the coast. On the nesting ground adult godwits have elaborate display flights, and are noisy; displays and calls are described in detail.

Information in this paper on the nesting cycle is based on 14 nests with eggs, at least 30 broods of chicks, and upwards of 80 pairs of breeding adults. The nesting season is marked by extreme compression of its several stages, to bring the young to maturity in the short Subarctic summer. The downy chick is described and figured for the first time. Adults withdraw from the nesting grounds in late July and move down the Hudson Bay coast preparatory to departure in late August for their wintering grounds. Juveniles follow about a month later, and apparently reach South America by the same route as the adults.

Acknowledgments

In addition to the several friends mentioned in the text as contributing field data to this paper, I am indebted to Mr. L. L. Snyder, Royal Ontario Museum, and Mr. David A. Munro, Canadian Wildlife Service, for the interest they have taken in my study of godwits, and to the Canadian Defense Department and its officers stationed at Fort Churchill for courtesies extended during my work on lands under their control.

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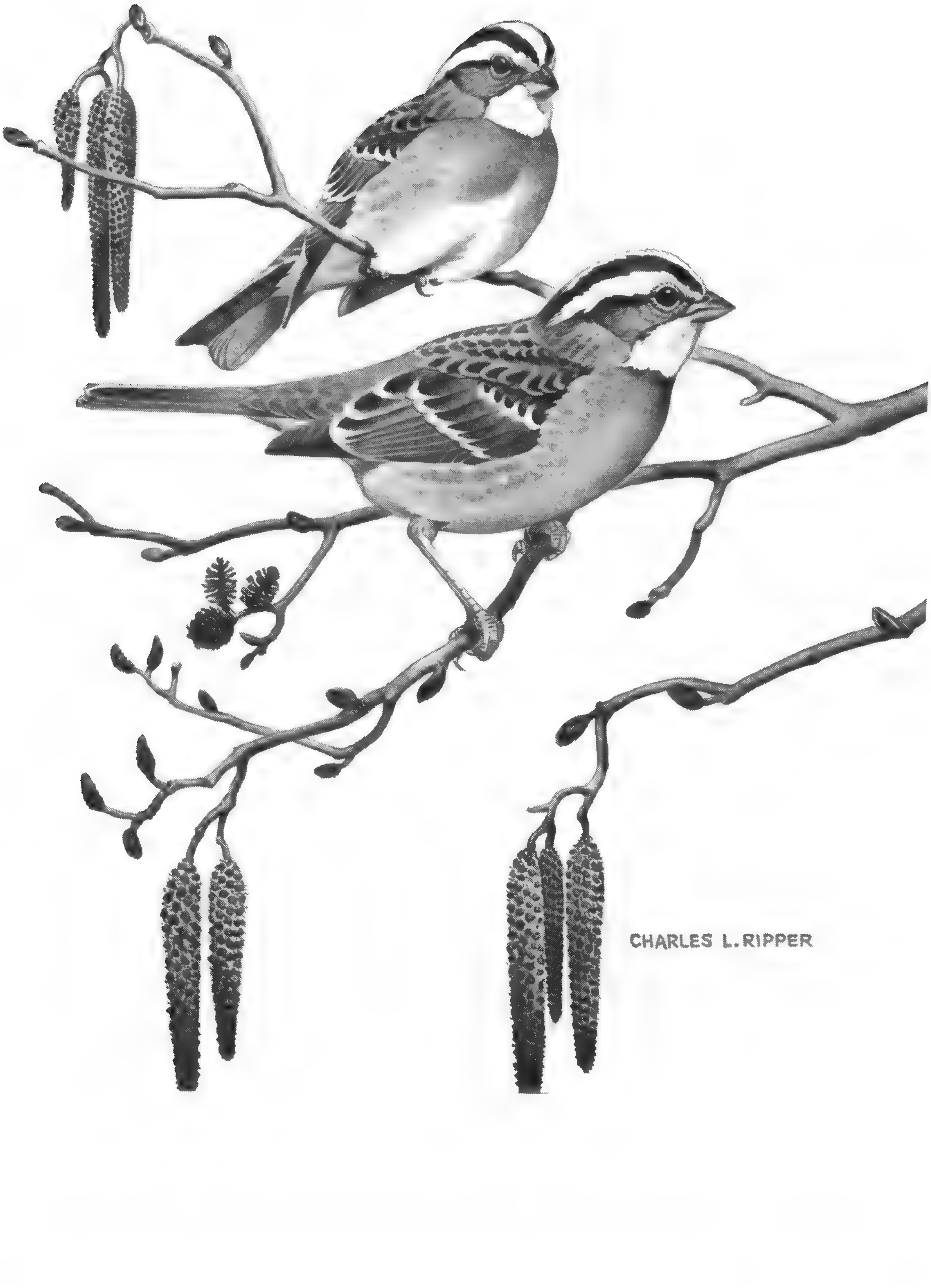
Scientific Names of Birds Not Given in the Paper

Arctic Loon	*Gavia arctica*
Canada Goose	*Branta canadensis*
Pintail	*Anas acuta*
Marsh Hawk	*Circus cyaneus*
Willow Ptarmigan	*Lagopus lagopus*
Semipalmated Plover	*Charadrius semipalmatus*
Killdeer	*Charadrius vociferus*
American Golden Plover	*Pluvialis dominica*
Black-bellied Plover	*Squatarola squatarola*
Ruddy Turnstone	*Arenaria interpres*
Common Snipe	*Capella gallinago*
Whimbrel	*Numenius phaeopus*
Willet	*Catoptrophorus semipalmatus*
Greater Yellowlegs	*Totanus melanoleucus*
Greenshank	*Totanus nebularia*
Lesser Yellowlegs	*Totanus flavipes*
Knot	*Calidris canutus*
White-rumped Sandpiper	*Erolia fuscicollis*
Least Sandpiper	*Erolia minutilla*
Dunlin	*Erolia alpina*
Short-billed Dowitcher	*Limnodromus griseus*
Stilt Sandpiper	*Micropalama himantopus*
Semipalmated Sandpiper	*Ereunetes pusillus*
Northern Phalarope	*Lobipes lobatus*
Bonaparte's Gull	*Larus philadelphia*
Snowy Owl	*Nyctea scandiaca*
Horned Lark	*Eremophila alpestris*
Tree Sparrow	*Spizella arborea*
Lapland Longspur	*Calcarius lapponicus*
Snow Bunting	*Plectrophenax nivalis*


CHARLES L. RIPPER

White-throated Sparrow, *Zonotrichia albicollis*. Drawing by Charles L. Ripper.

THE BEHAVIOR AND ECOLOGY OF THE SOUTH AFRICAN OSTRICH

E. G. FRANZ SAUER and ELEONORE M. SAUER

Photographs by the authors in 1964

Since the Lower Pliocene Epoch at least nine species of ostriches of the genus *Struthio* roamed the Ethiopian, Palearctic, and Oriental Regions. Their fossil relics are spread from western Asia, to Europe, to southern Africa, and eastward to China and Mongolia, reaching as far north as 50° N Lat. Further, *Eleutherornis,* representing a Middle Eocene genus from Switzerland, is described as another member of this order. *Psammornis* from North Africa and Arabia and *Eremopezus* from the famous Fayum formation of Egypt, too, may eventually become classified with the ostriches and no longer with the elephant birds, the Aepyornithidae.

Only one species of ostrich, *Struthio camelus,* the last of the whole order Struthioniformes, survived to the present day with several subspecies on the African continent. This modern bird appears in the fossil record as a neospecies in the Pleistocene. Its Syrian subspecies, *S. c. syriacus,* became extinct as recently as 1941 (Meinertzhagen, 1954), and on the African continent, which is changing so rapidly at present, wild Ostriches have disappeared in vast areas where they thrived only a short time ago.

In contrast to the wild bird, the Ostrich as a domesticated farm bird and zoo specimen is closely approaching the status of a cosmopolitan species, though split into a great number of rigorously isolated populations from large to extremely small. Man has relied heavily on this fenced-in creature to describe the general biological features and functions of this the largest of all living birds. Until a short time ago he has neglected any scientific study of the flightless Ostrich in its wild state.

Beguiled by a glimpse of its secret family life in the wilderness of South West Africa, we (F. Sauer and E. Sauer, 1959) began a systematic study of the life of the wild South African Ostrich (*S. c. australis*) in the arid South West African veld. In 1964, the National Science Foundation supported our research through grant GB-2167, and we were again happily assured of the friendship and help from our many South West African friends and government officials.

While we are preparing a monograph on the behavior and ecology of the wild Ostrich, we have nevertheless accepted with great pleasure the request by O. S. Pettingill, Jr. to publish this short report of our study for the readers of *The Living Bird.*

The Study Areas and Methods

Arid South West Africa is composed of three major regions, the coastal Namib Desert, the mountain ranges and high plateaus that are defined in the west by the Great Escarpment, and the Kalahari Basin which, in its northwestern section, reaches toward the Kaokoveld and includes the drainless Etosha Basin (see Figure 1). The latter yielded the fossil shell remains of the giant "oshana" ostrich, *Struthio oshanai* (Sauer, 1966b).

Wild Ostriches in fluctuating numbers are still found in each of these three regions, and we collected data on their life history in all three. Nevertheless, in several vast districts within these major regions the Ostrich has disappeared. The establishment of a farm zone in the mountain region and on the high plateaus may be the major reason for the disruption in the distribution of the Ostrich and has now led to the establishment of isolated Ostrich populations. For example, in the vast and dry southern part of the country, where once an accidental discovery of precious diamonds in the gizzard of a dead Ostrich triggered the devastation of this bird, we found no trace of its presence. Still, most of the farmers appreciate the wilderness of their beautiful country and try to preserve this unique bird even though they vaguely accuse it of eating every day as much as a horse eats.

Wild Ostriches are alert and extremely shy. The success of any close observation depended on perfect camouflage of ourselves and our equipment — field glasses, a spotting scope, ciné and still cameras, and a tape recorder. We imitated termite mounds, natural rock formation, and plant growth. Our termite mound camouflage proved to be most efficient; we used "stationary" and "walking termite mounds" of different shapes, colors, and textures according to the varying local patterns and colors of natural mounds. In fact our camouflage was occasionally so perfect that an Ostrich and even oryx gazelle (*Oryx gazella*) urinated and defecated onto our termite mound while we observed and photographed from within. There was, however, a slight disadvantage to such a perfection when venomous snakes sought shelter from the heat in our hollow termite mound. According to our experience, South West Africa seems to be indeed one of the world's foremost snake countries. When checking the work area and keeping single nests under continuous observation, we also used other lookouts, such as trees, a nest of a Black Vulture (*Torgos tracheliotus*) strong enough to house comfortably at least two adult human beings, rocky rises, mountain peaks and slopes, and even the roof of the Volkswagen Bus.

Our main study was conducted in the uninhabited inner Namib Desert within Game Reserve 3 (Figure 1) where, in 1964, we found an exceptional number of Ostriches — more than 1,500 — gathered in the neighborhood of two water holes during the dry season. Then we observed a geographically isolated population of less than 50 Ostriches on the high plateau of Ombu in the Erongo Mountains. We also made comparative studies in the different biotopes of Etosha Pan, Kaokoveld, and in the Sandveld (Omaheke) of the Kalahari region.

Adaptability of the Ostrich to Arid Habitats of the Veld

We selected study areas in various lowland and mountain habitats to investigate the Ostrich's adaptability to various biotopes and the influence of the different environments on its daily behavior and annual activity rhythm. We found that the Ostrich inhabits diverse ecological niches ranging from vast sand flats, grasslands, and very open bushveld to the dense thornbush veld, to *Mopane*-woodland, and even to steep and rugged mountain habitats where its proverbial running speed is replaced by an astounding ability to climb quickly over gravel fields and rocky rises.

While the annual cycle of cold-dry and warm-rainy seasons with their many variable environmental factors imposes on the Ostrich an annual rhythm of behavioral motivations and social organization, both the South West African climates and the Ostrich itself proved to be most unpredictable in fluctuating and deviating from the norm. And, while the reproductive activities of the Ostrich reached their peak at the beginning of the rainy season, which occurred at different times in the different study areas (and also may vary considerably from year to year in the same place!), we found some successful new offspring at any time of the year, even in the coldest month. The Ostrich appears as a highly adaptable and successful opportunist breeder in a climate where this is of greatest biological significance. Various other behavioral phenomena, too, indicated the Ostrich's high adaptability and quick response to local environmental changes — e.g., to a locally very restricted, short, and untimely rainfall. Different ecological conditions in the different study areas were responsible for significant behavioral differences in the daily and yearly activity patterns of the populations under study. While the Ostrich responded with various behavioral adjustments in a given location, it performed extended migrations when worse came to worst.

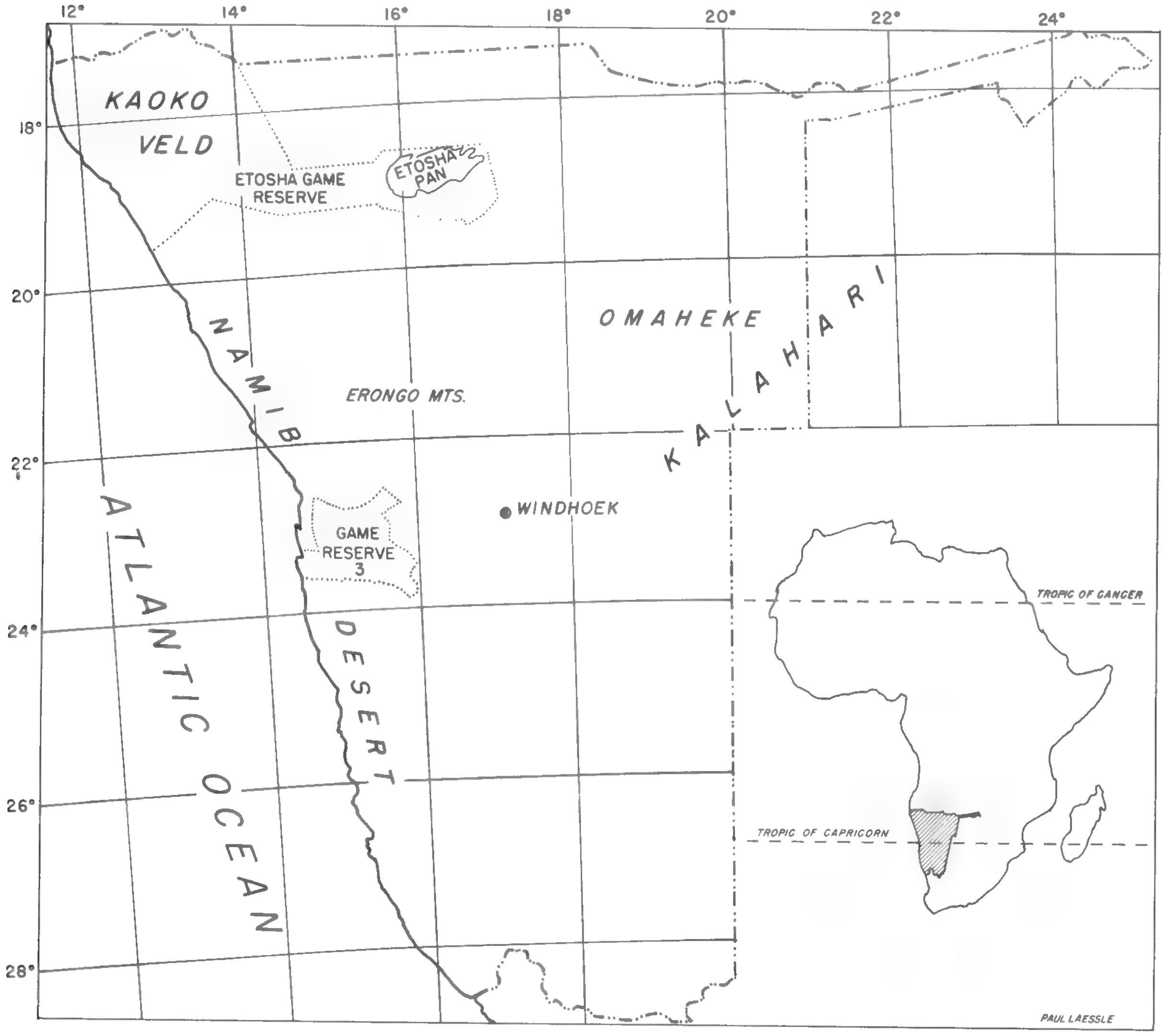

12°
14°
16°
18°
20°
22°
24°
18°
20°
22°
24°
26°
28°
KAOKO VELD
ETOSHA GAME RESERVE
ETOSHA PAN
NAMIB DESERT
ERONGO MTS.
OMAHEKE
KALAHARI
WINDHOEK
GAME RESERVE 3
ATLANTIC OCEAN
TROPIC OF CANCER
TROPIC OF CAPRICORN
PAUL LAESSLE

Figure 1. Map of South West Africa showing the Namib Desert, Erongo Mountains, Etosha Pan, and Omaheke where the Ostriches were studied.

The broad adaptability and immediate responsiveness of the Ostrich to extremely fluctuating environmental conditions are of greatest biological significance for the survival of the species. Furthermore, these mechanisms are the very basic biological substrate so highly desirable for any wild animal chosen for possible domestication by man (Sauer, 1966a).

The Pattern of Social Organization

Age and internal motivations, as well as biotic and abiotic environmental factors, influence and change the group life of the Ostriches significantly in the course of the year, and sometimes even during a single day.

When the annual seasonal rhythm follows closely the normal sequence of one cold-dry and one warm-rainy season, one finds during the cold and dry months most of the Ostriches associated in "superfamily" units up to the size of herds. Family groups with and without chicks, as well as assemblies of immatures of both sexes, dominate during the rainy season. This statement, however, is very schematic and generalized; the social structure of an Ostrich population is usually more complex and differentiated throughout the year. On one hand, the annual climatic rhythm rarely follows the rule. The timing of rain fluctuates widely and is usually very unpredictable. When it comes, rain is often sporadic and locally very restricted. Further, the longevity of the Ostrich, differential effects of variable climatic conditions on different age groups, and different social attitudes of immatures, adult cocks, and adult hens — to mention a few factors — add to the complexity of the Ostrich community.

Areas around water holes usually serve as communal pastures for mixed herds of adult and immature males and females (Figures 2 and 3). Well-established family and superfamily groups approaching the water from various directions often fuse temporarily in these community centers. In Game Reserve 3, some of these Ostrich assemblies at the water holes numbered more than 600 at a time during the dry season.

Within the social groups, adult "major hens" or adult cocks play a leadership role. To mention a few examples: They signal the group to move on in a given direction (Figure 4) or to stay in an area for temporary grazing. They may decide on when and where to take dust-baths and they may flush the birds that try to form a community bath on their own at the wrong time in the wrong place. While firmly leading the group in familiar territory, a major hen will drastically change her behavior when the group finds itself in strange territory or in the neighborhood of a water hole bare of animals. In such situations the Ostrich flock usually senses danger and immediately is reluctant to move on. The birds stand crowded and alert for a while, listen, and look around. When they manage to suppress a hasty flight in favor of their desire to advance, a major hen may give a most significant display of "sacrificing the socially lower ranking companion." Sometimes she is supported in her action by several other adult females and males, or one of these, anxious to get to the water, will perform this display. She will turn around and walk back to get behind one or several inexperienced immatures, utter muted threat calls, ram, kick, and push them to advance first and possibly "spring the trap." The biological significance of this behavior is very evident; it averts pending danger from the adult bird to an inexperienced individual of lower social rank. Immatures, however, learn from repeated experience, and, if a major hen chooses the wrong bird as a "scapegoat," it may avoid the hen by quickly turning around and speeding away in the opposite direction. This usually makes the whole group follow in "blind terror."

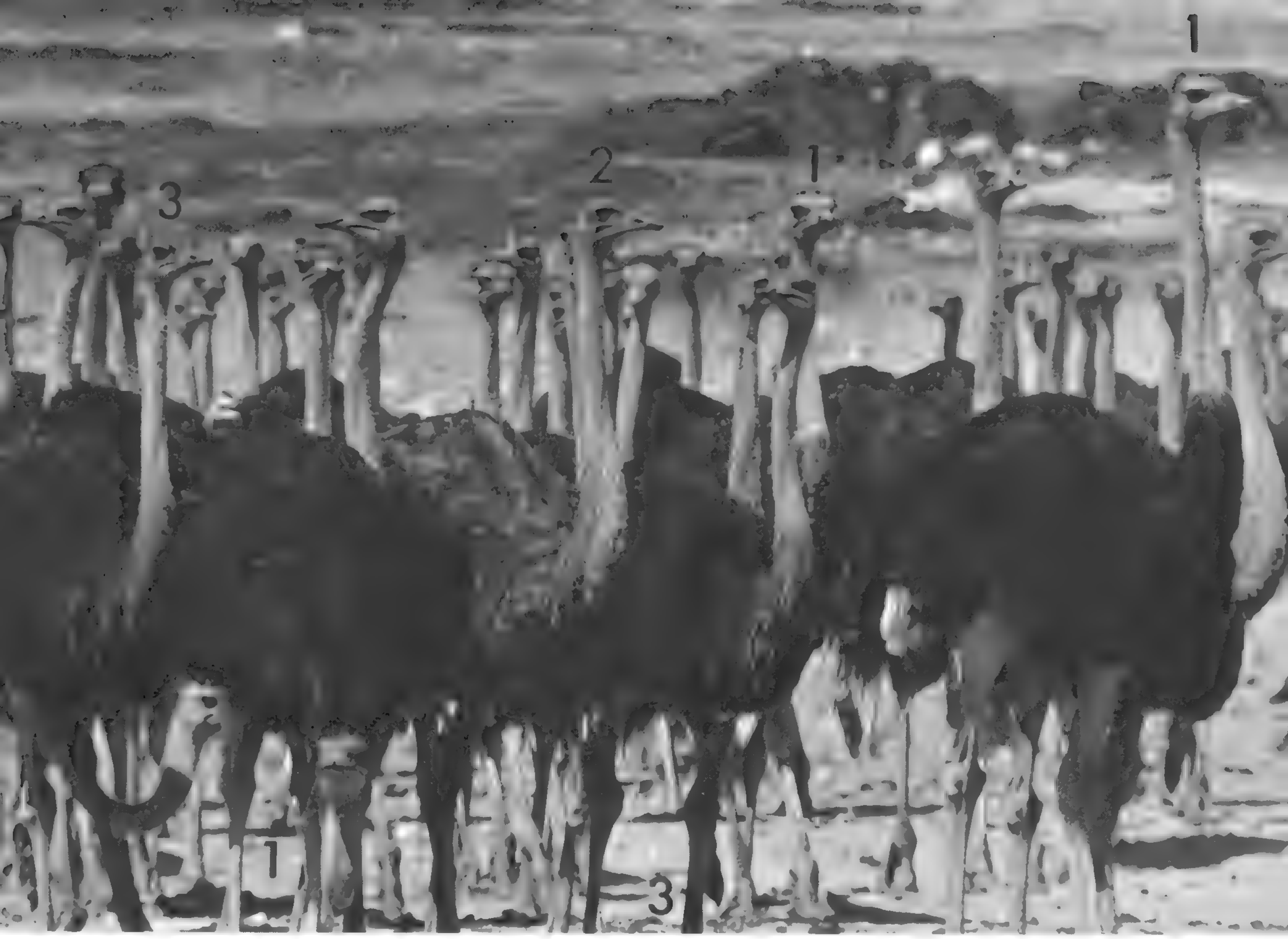
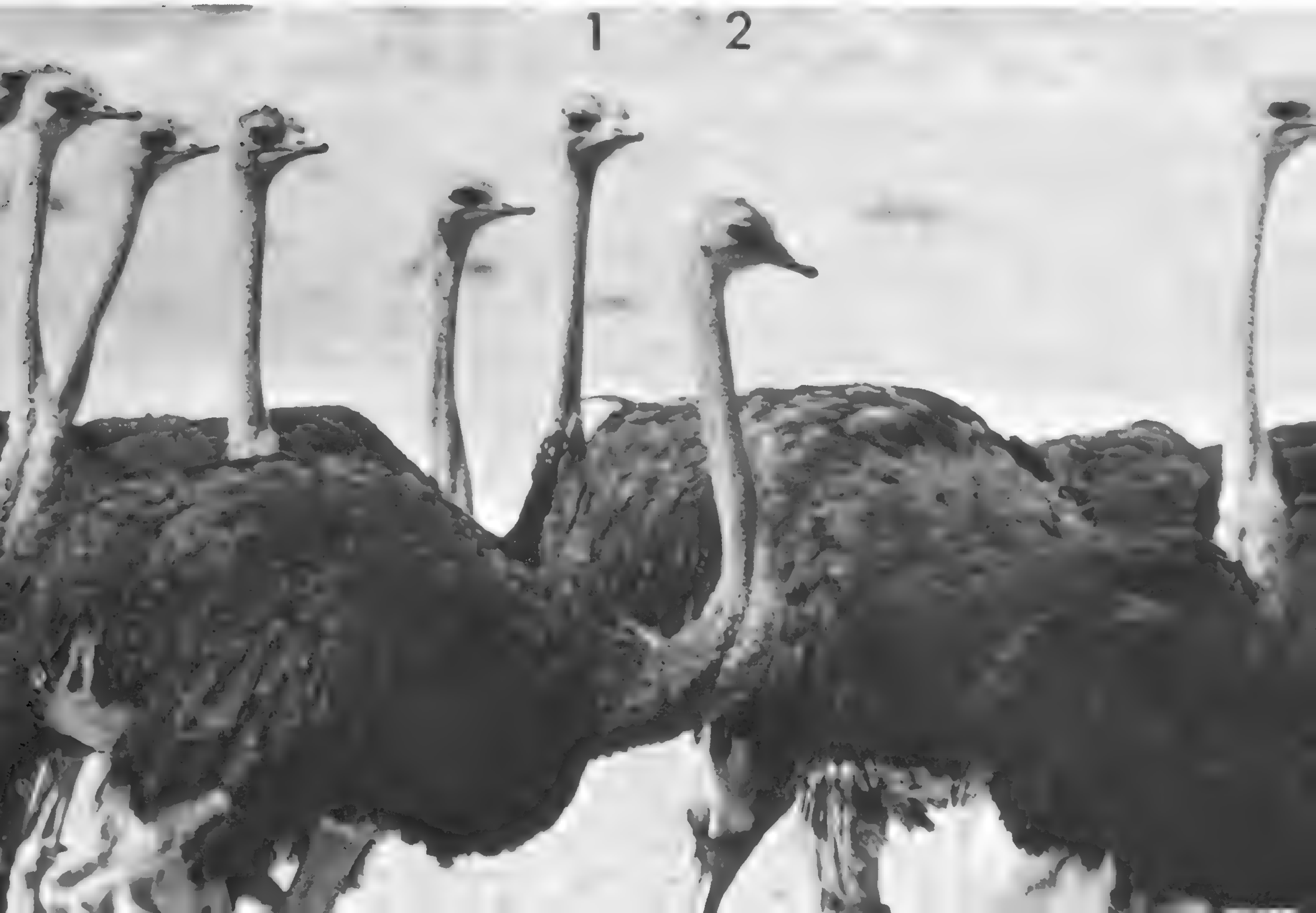


Figure 2 *(above)*. A small fraction of the Ostrich herd on the dry bed of the Hotsas River in Game Reserve 3, Namib Desert, 17 August. Birds numbered: 1, maturing males; 2, maturing females; 3, one-year-old bird.

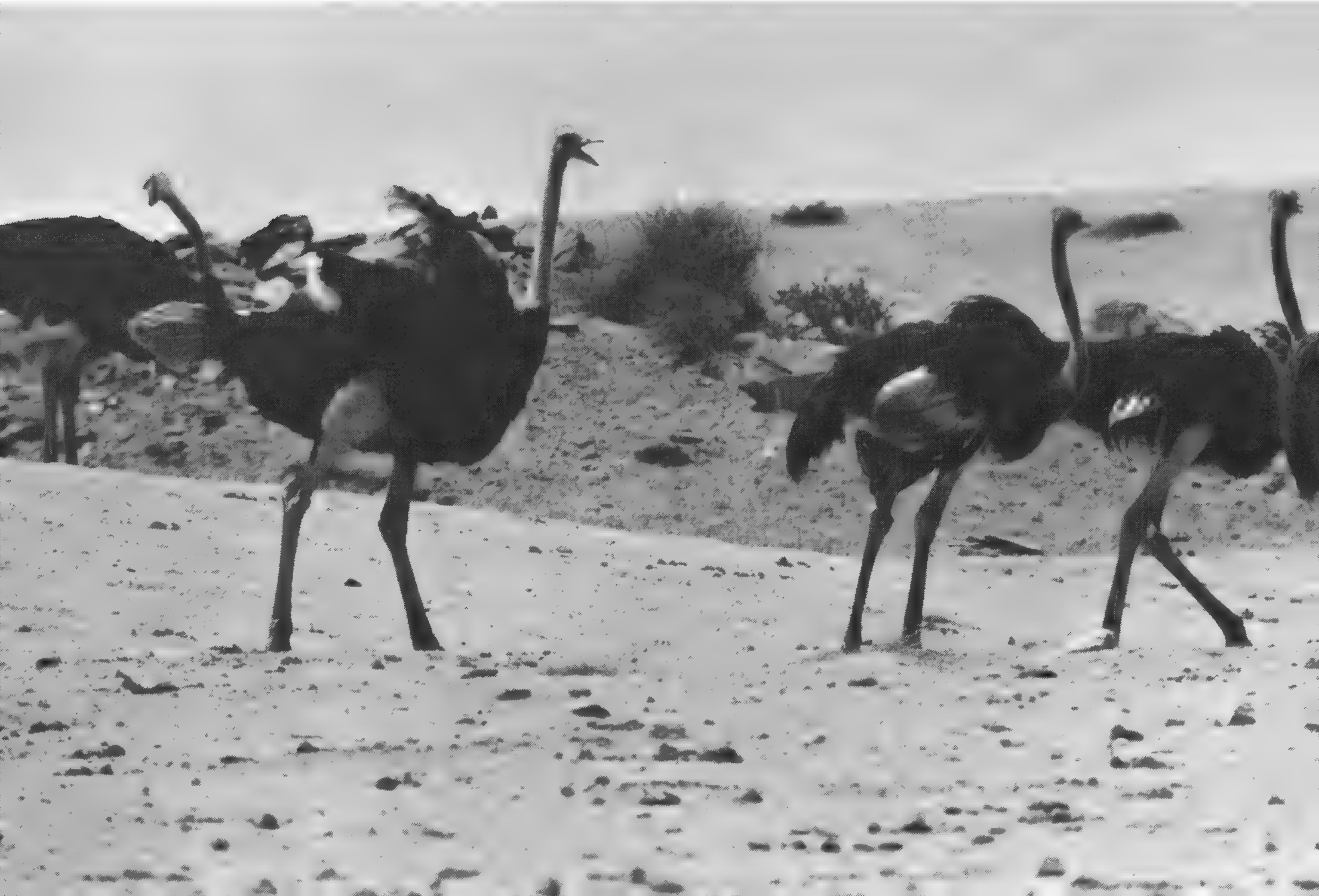
Figure 3 *(below)*. Maturing males and females approaching a water hole. Numbers 1 and 2 are male and female, respectively. Hotsas, 14 September.



The individual birds within a large herd maintain close social contact with the companions of their original social group, and they disperse again into their close-knit family and superfamily units when leaving the watersites. Nevertheless, the temporary large herds, often forming and disintegrating day after day in the neighborhood of water holes, are not simply pseudosocieties. Much inter-group communication takes place within the herds. Such important social contacts are initiated and established as acquaintance between individuals from different families, adoption of stray immatures by existing family units or, significantly, by solitary maturing males. We found further that pairing of maturing and adult birds, the formation of polygamous and monogamous marriage bonds, and rivalries as well as various ceremonial displays between individuals and between groups may take place within the herd (Figure 5). Under the protection of a large herd surrounding a water hole, tired individuals and groups, that have come a long way from their family territories, find time to rest and even for deep sleep. Relaxed birds, performing extended comfort behavior, are commonly seen when the groups wait for their turns to get to the water (Figures 6-12).

Many more social functions are tied to these large temporary aggregations. In moments of confusion caused by fear and easily triggered by oryx gazelles, Pied Crows *(Corvus albus)*, and other animals, the members of a single social unit will sometimes disperse in various directions. Adult males frequently manage to herd their mates in their own escape directions by performing elaborate "flash" displays. While running at full speed suddenly they zigzag toward and away from their mates, throw their wings high, sometimes trying to get behind a mate, and then running away again, often

Figure 4. An adult male Ostrich second from left, signals his flock of immatures to advance after a rest. Here his display equals a "moderate threat" to which the second immature bird from the left responds by lifting its tail and advancing with a quick step while uttering a muted fear note. Not a member of the advancing flock, the adult male at far left continues preening. Hotsas, 16 September.



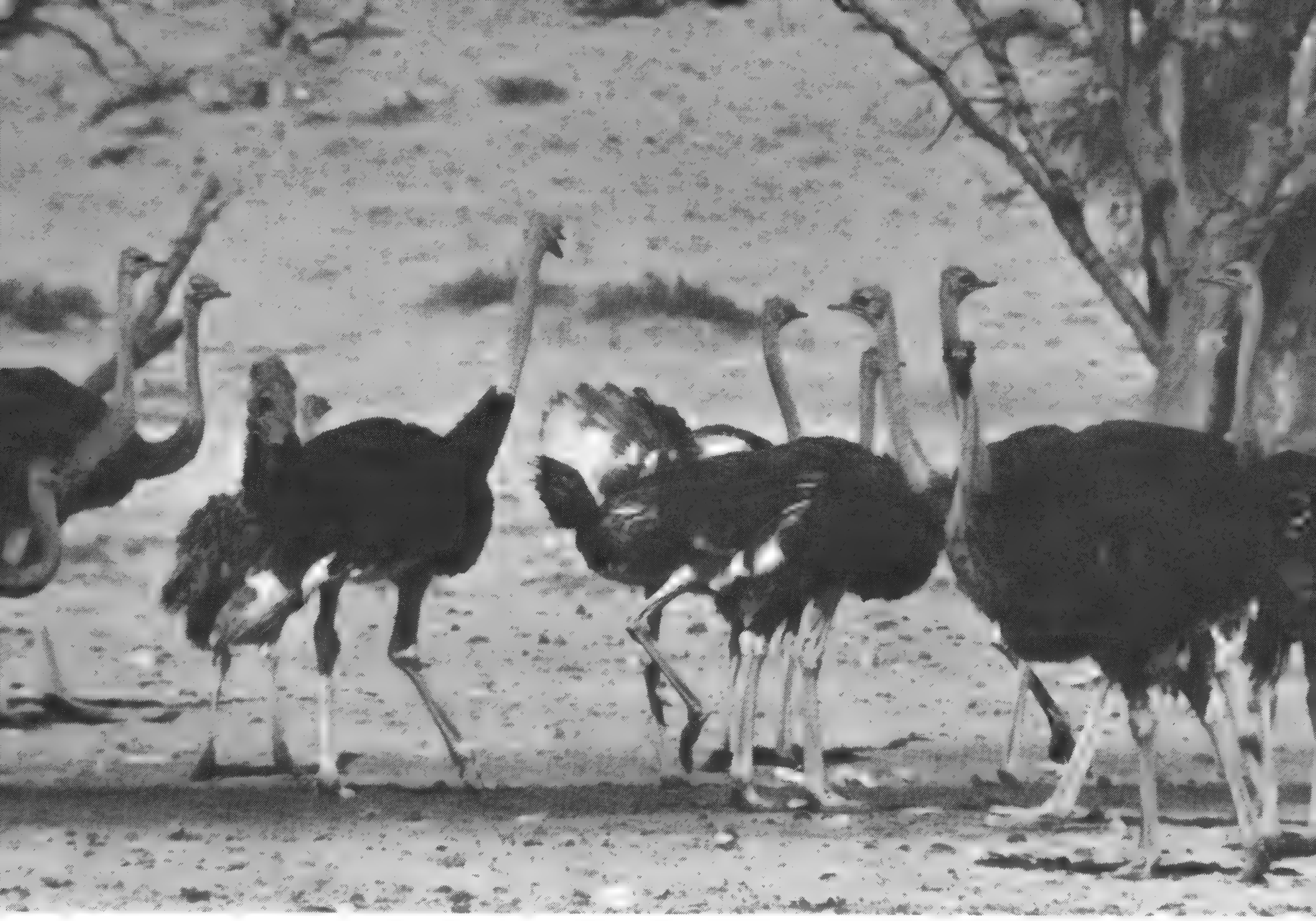


Figure 5. An adult male Ostrich, while leading his flock, chases a group of immatures from the watering site. A small, approximately five-months-old bird stands close to the cock where it finds protection from sudden attacks by other Ostriches. Hotsas, 19 August.

uttering notes of fear and threat. At last, when the danger and disturbance have passed, members of a group quickly find their way back to unite with one another again. Their unification is obviously based on individual recognition of conspecific partners and on an ability to orient themselves toward their family or superfamily territory or pasture, which may be 50 miles or more from the water.

The social units that persist during the dry season—some even longer—are quite diverse in their structure. To mention only a few examples: Two adult males may live with 100 and more immatures, and they may be seen flanking the herd on the right and the left, while the group grazes and slowly moves about. Various numbers of adult males and females can form a social unit, or they may live with immatures of the first, second, and third year. One- and two-year-old immatures without adults may form a society. Maturing males and females may associate. Even 30, 40, and more adult males may herd together very peacefully until sexual motivation breaks up the group. And during the nesting period two neighboring males may join for their long walks to and from the water, then separate quietly and return to their nest-sites without showing the slightest sign of hostility the entire time. New acquaintances are sometimes made rapidly and in almost unbelievable ways throughout the year. There are no rigid rules and any attempt to interpret the Ostrich's social structures can be doomed to failure when,it is based on short observation. Even a male, seen leaving a nest-site with a hen and a flock of chicks, may not have fathered a single one of the fledglings, and his very recent and peaceful association with the group may be the result of an acquaintance with the hen long before the reproductive season and may have been possible because her original mate left her alone.

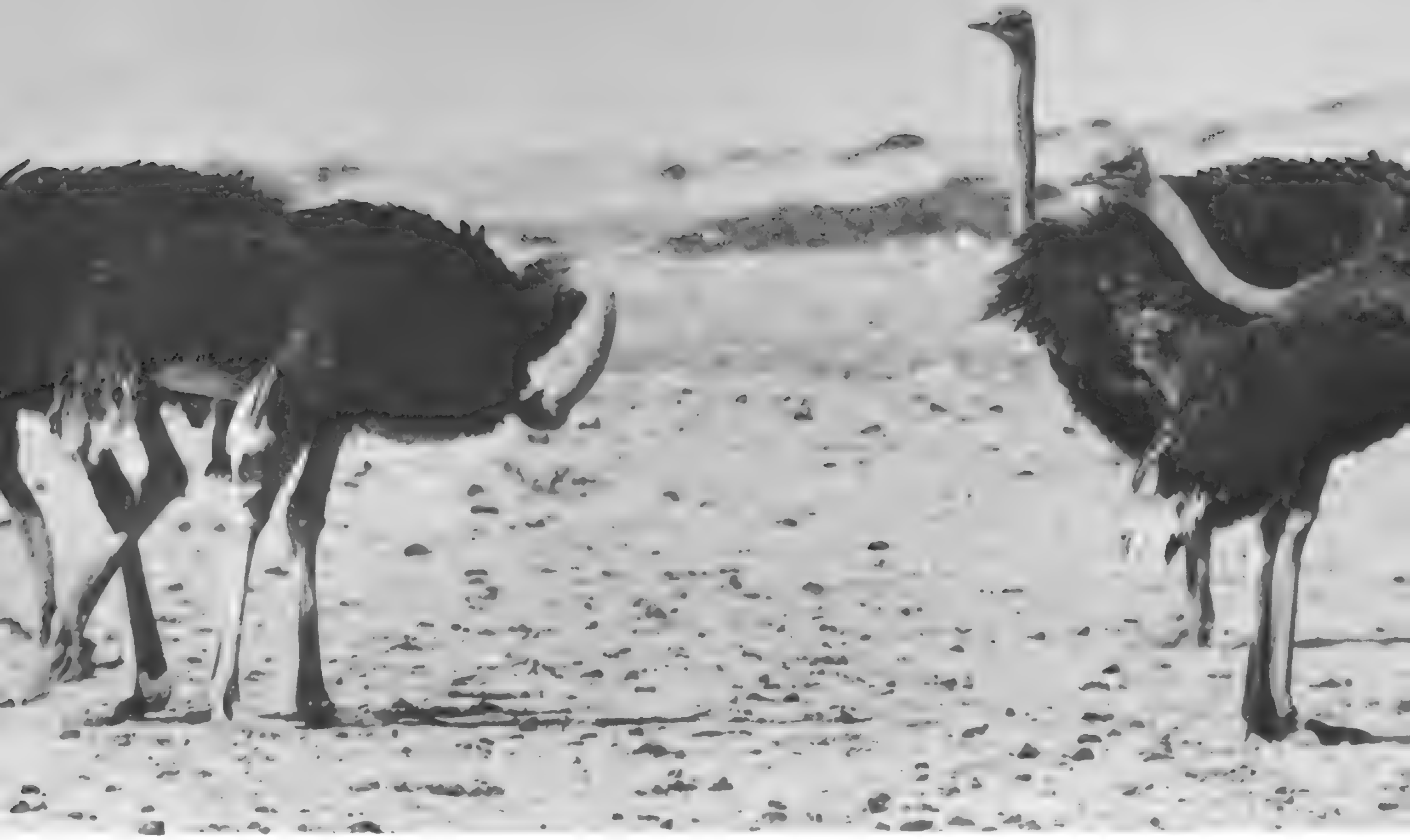
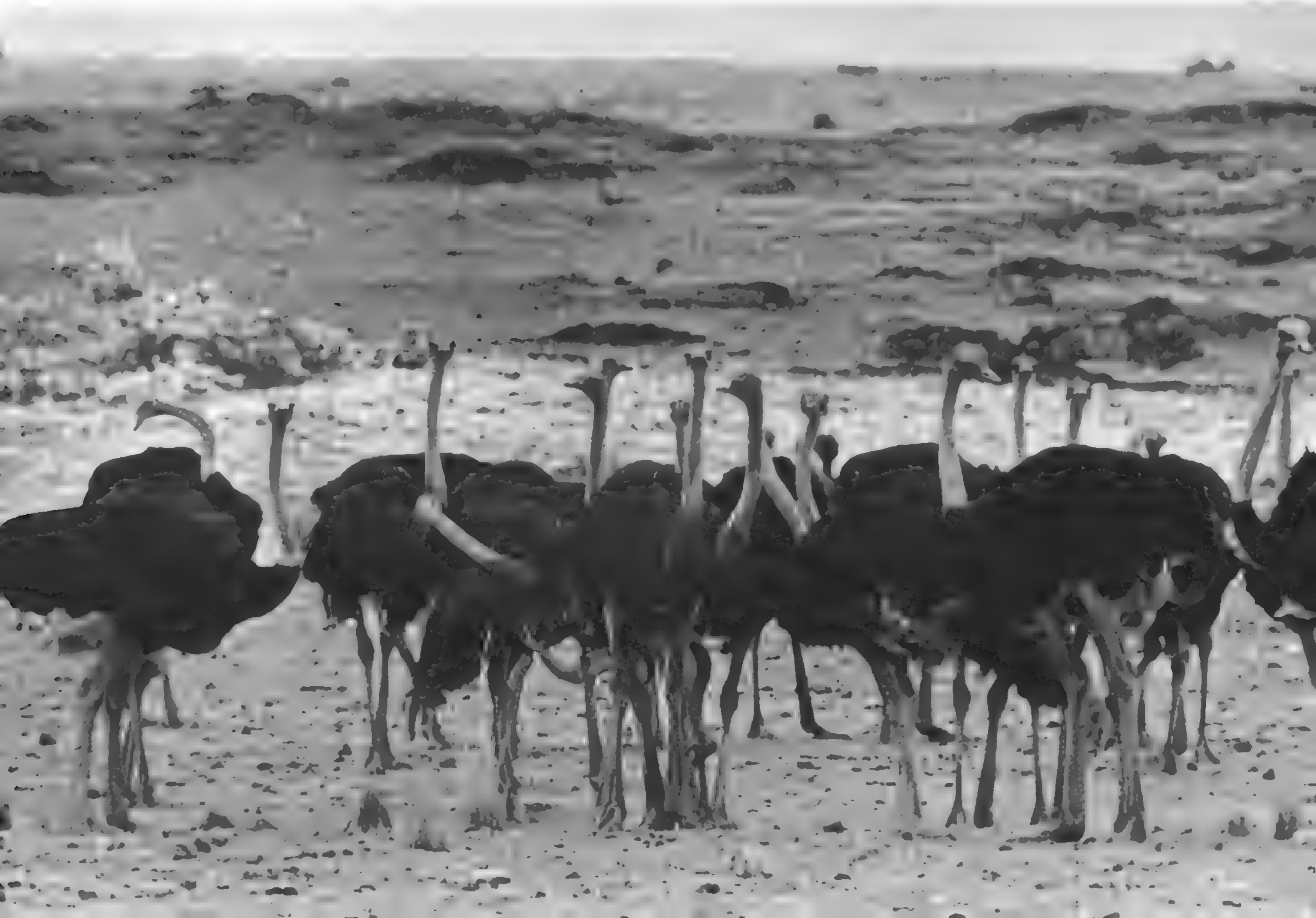


Figure 6 *(above)*. Four young but mature female Ostriches resting and preening. One is rubbing her throat with the side of her foot. Hotsas, 5 September.

Figure 7 *(below)*. Adults and immature birds of both sexes resting and preening. Hotsas, 18 October.



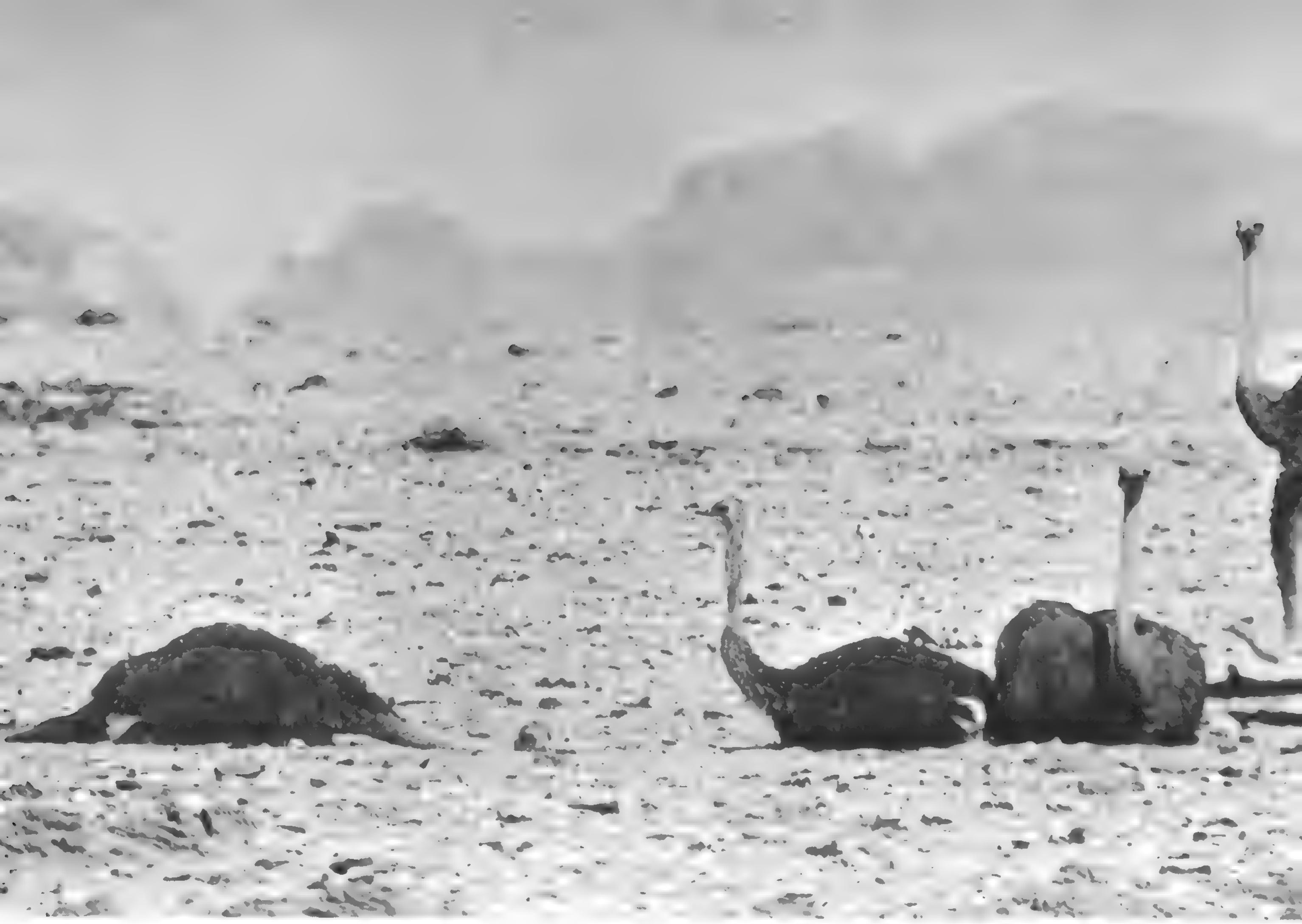
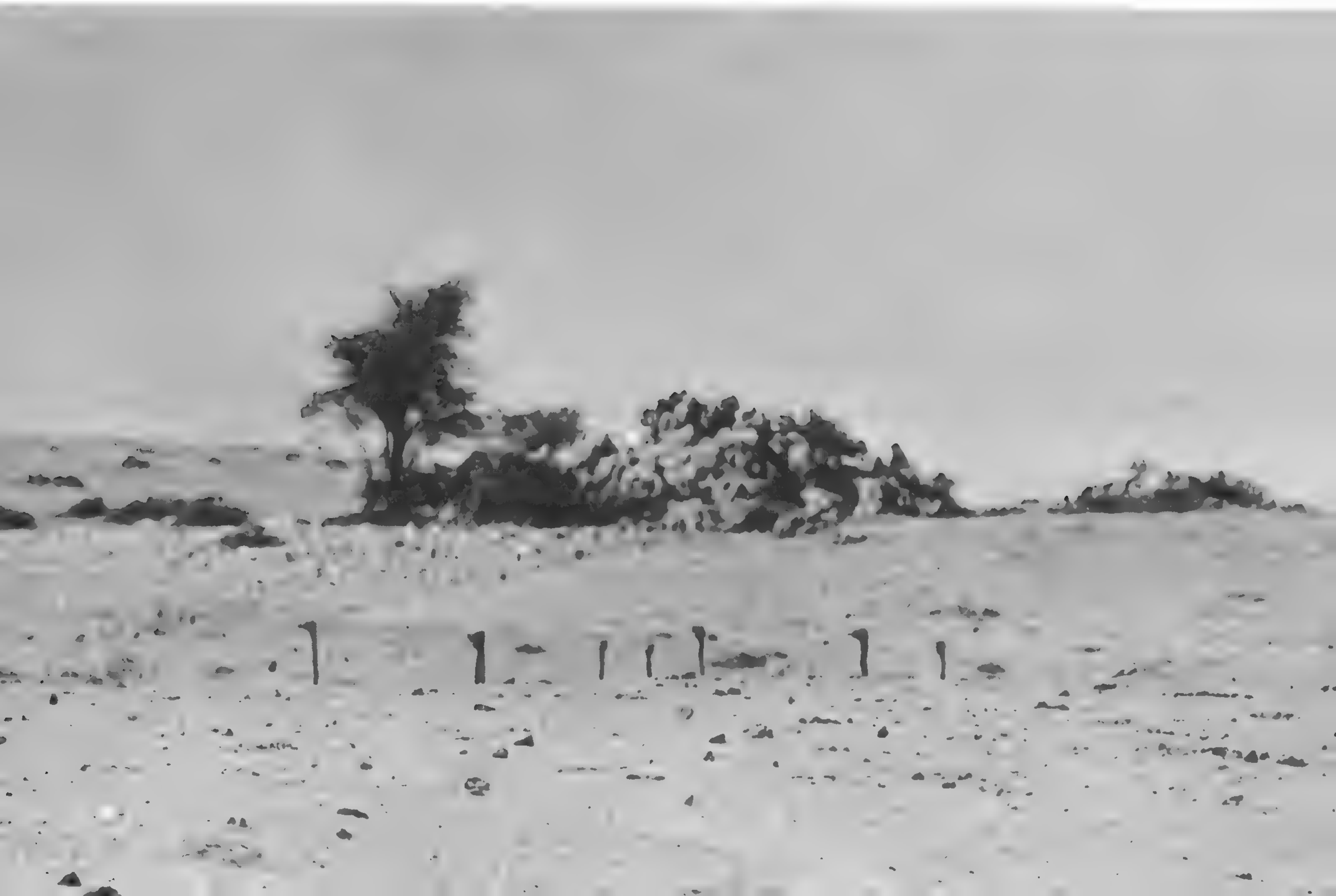


Figure 8 *(above)*. Sleeping and resting Ostriches, approached by a flock of immatures of which the first has assumed the subordinate posture, thereby avoiding hostile encounter. Notice the effect of camouflage by ruptive pattern. The head and neck of the sleeping young hen blend with the background while the body, seen from a distance, looks like one of the scattered salt bushes, with the tail resembling the shadow cast by the sunlight. Ganab in Game Reserve 3, Namib Desert, 14 July.

Figure 9 *(below)*. A flock of Ostriches, with only their heads in view, dust-bathing in their "community bathtub." Hotsas, 5 September.



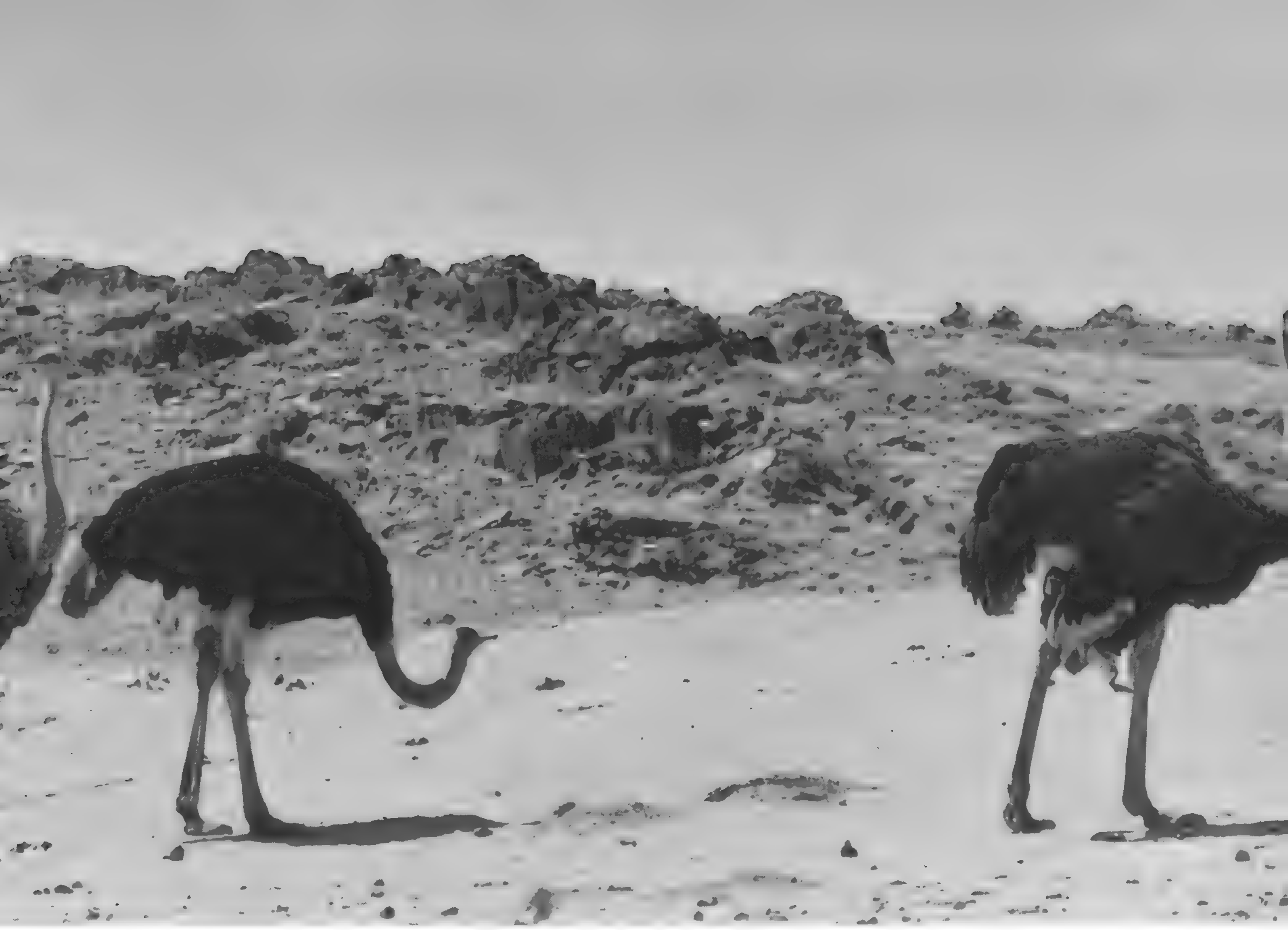
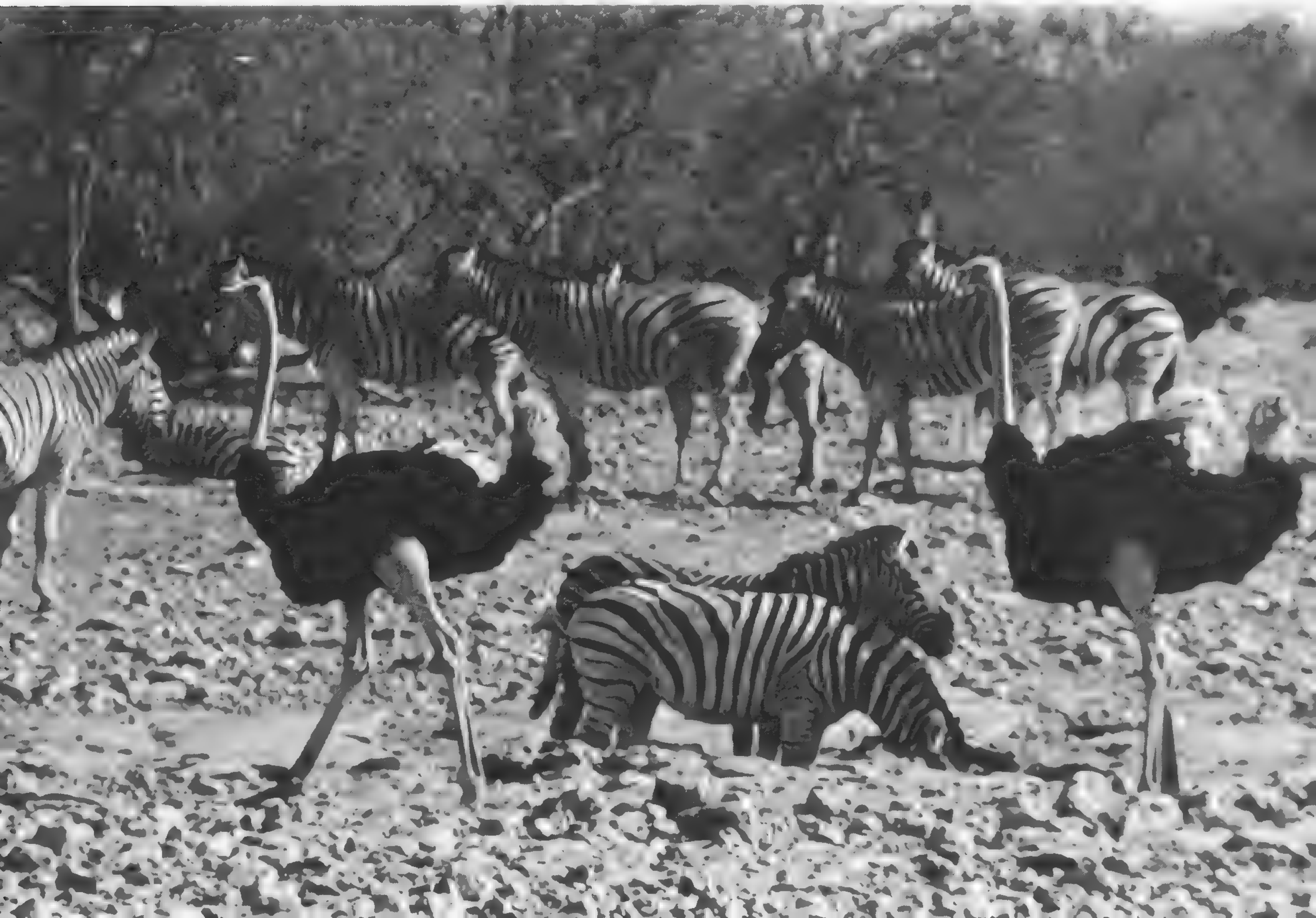


Figure 10 *(above)*. Solitary male in subordinate posture passes resting birds. From left to right: adult female; adult male; young male whose sigmoid-shaped neck is in resting position. Hotsas, 16 September.

Figure 11 *(below)*. Two excited adult male Ostriches, equal in social rank, circling the Ombika water hole occupied by Burchell's zebras. Etosha Game Reserve, 11 November.



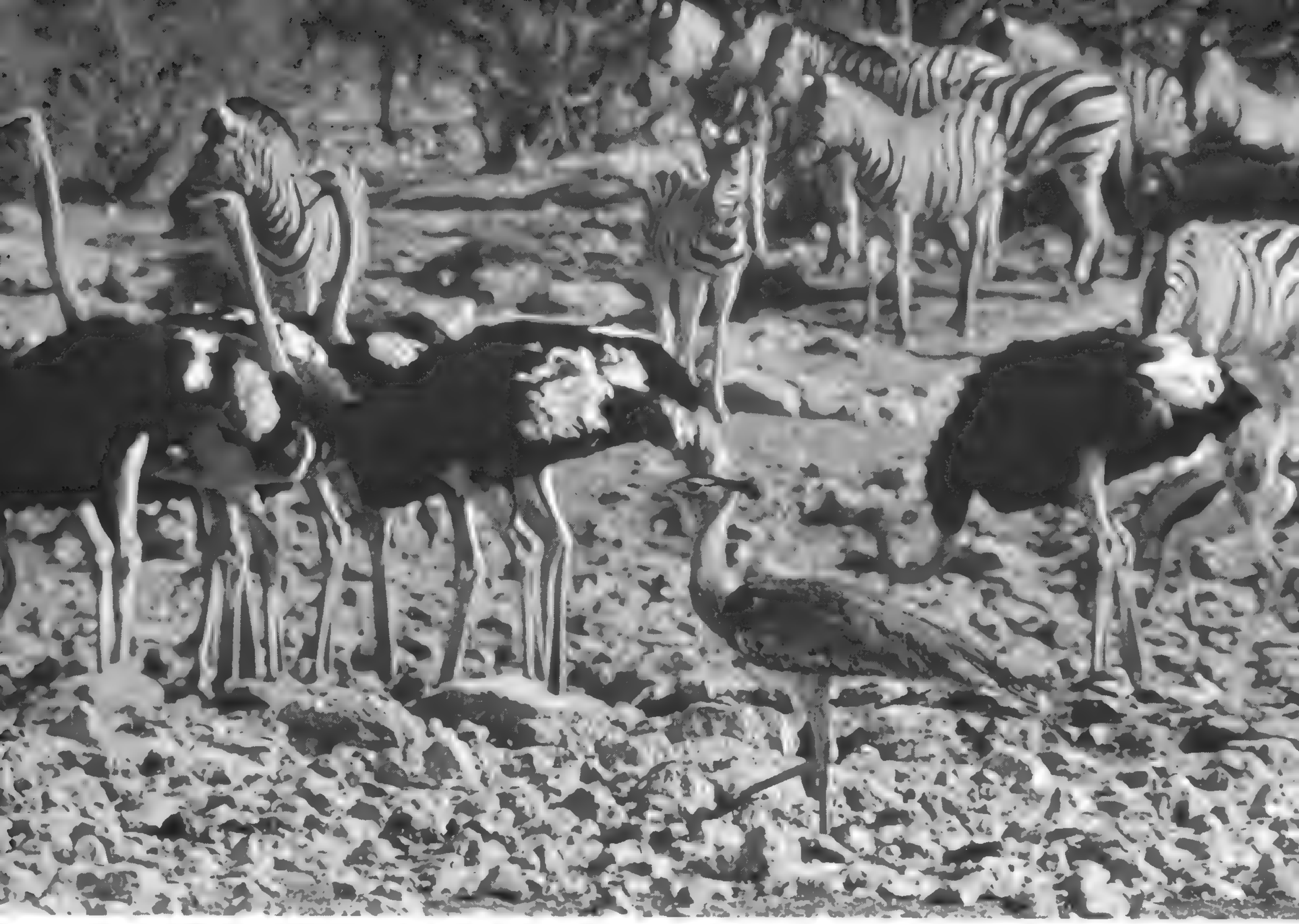
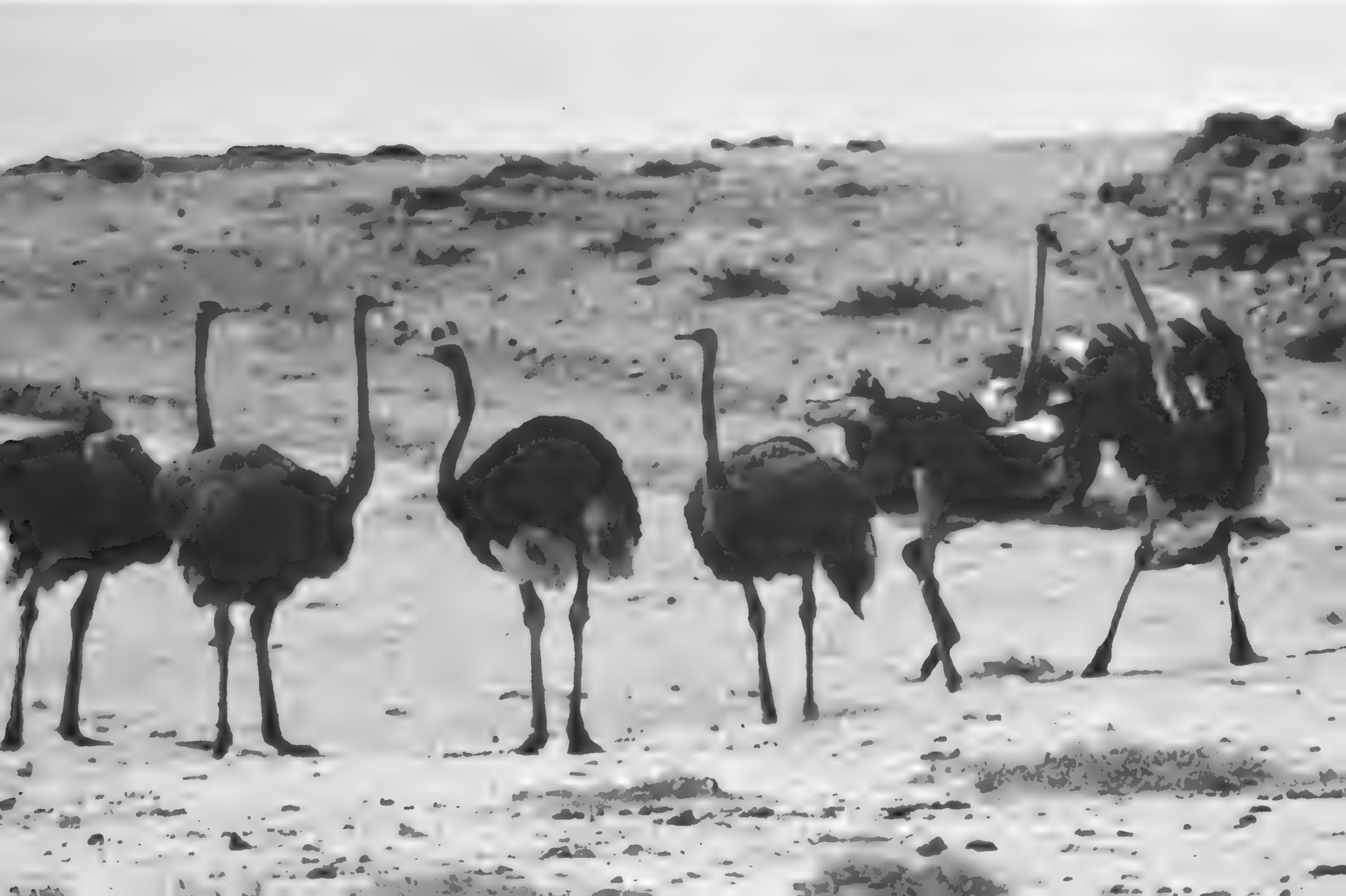


Figure 12 *(above)*. After the zebras have quenched their thirst, the Ostriches close in on the water. But holding a low rank in the interspecific rank order, they are already alerted by the appearance of a springbok *(Antidorcas marsupialis)* and a Kori Bustard *(Choriotis kori)*. Ombika, Etosha Game Reserve, 11 November.

Figure 13 *(below)*. Beginning of the Ostrich's reproductive cycle. An adult hen chases a maturing female away from her family. While the adult hen next to her and the cock, too, remain calm, the third hen brings her tail up and watches the attack in excitement. The maturing male next to the third hen is alerted. Hotsas, 16 September.



The Reproductive Cycle

Courtship

Most of the newly formed polygamous, less often monogamous, marriage bonds among Ostriches are founded near the water-sites within the large herds and quite obviously between birds of different social groups. Old-established family units frequently persist throughout the dry season. It is the role of the major hen to demonstrate her dominating family rank to associated "minor hens" and their mate. She also attacks an "undesired" minor hen and drives her away from the group (Figure 13) and, finally, when she becomes sexually motivated, she chases away all the offspring.

Most of the adults complete their molt into the nuptial plumage during the months of July and August. Thereafter, the reproductive cycle begins here and there, very sporadically, and affects more and more adult groups. When the food supplies have been lastingly rich in the area where the population lives, the main reproductive period builds up gradually. All this occurs towards the end of the dry season and long before the first rains fall. Many a family may complete successfully the whole reproductive cycle without having been exposed to a single shower of rain. While rainfall stimulates the birds to show reproductive activities, it does not have the value of an obligatory or even necessary releaser. The factors which build up the hen's reproductive potential and trigger her reproductive activities at the right time are predominantly the availability of sufficient food over a length of time and her social standing in the community.

It is well to remember here what we mentioned above, that individual families can begin their reproductive cycles and complete them successfully at any time of the year when the internal readiness is given and triggered by suitable stimuli.

Mature hens commonly begin and complete their molt some time ahead of the cocks and then initiate prenuptial courtship activities. They will posture and stand very erect, urinate and defecate, and otherwise behave in exaggerated manners in front of potential or familiar mates. They peck, kick, and drive other females and males away from the neighborhood of the males they are courting. Uttering threat calls, they dash in an exaggeratedly fierce manner, particularly toward any immature bird that peacefully passes the scene. The latter usually assumes very quickly the characteristic subordinate posture—head low, neck U-shaped, and tail down—that immediately disarms the aggressor. The hens are also very efficient at inciting fights between adult males. This happens at the time when the last old family units break up; the yearlings, repeatedly driven away by the fierce adult hens and successfully rejoining the family for a number of times, finally give up their attempts and begin to lead their own group life.

In the development of these courtship displays, the males are late in coming into the picture—not until the red pigment appears on the surface of their shins and feet and in their faces. This color is quite a contrast to the dark pigmentation on the legs of the sexually stimulated hens (Figure 14). While still in the herd, they gradually give up their (perhaps only simulated) disinterest in the females' preliminary courtship activities. They show more and more often ceremonial rivalries between each other, sometimes chasing around in groups, wings held high, and "dancing" in flocks numbering up to 40 and 50 individuals (Figures 15 and 16). In another ritualized display, they chase females around with their wings held high or waved alternately right and left, and the bushy tail held high and bent forward (Figure 17). A strong cock may display his social dominance in the flock (Figure 18), particularly in the presence of other flocks with sexually motivated males. He may be standing very erect and his tail pointing up, meanwhile addressing passing birds with a hiss, a snort, a muted *boo,* or other threat calls. If his dominant position is respected on the levels of intra- and inter-group relationships, no other male around holds his tail as high as he does. The next highest ranking cock may keep his tail just slightly above or in the horizontal plane, while the other males in subordinate positions or entirely disinterested in the game hold their tails at various angles downward or in a drooping position. Thus, the position of the tail of an Ostrich is an excellent indicator of the mood and social position of the bird. Some dominating males maintain their alert posture for hours without eating a single morsel of food until the rival males have left and they can relax. At this time in the priming of their sexual drive, the males' cloacal wall and the penis turn bright red, a vivid contrast to the pale color of these parts in sexually inactivated adult or maturing males. Having reached this level of excitement, the males frequently give their penial displays, a ceremony associated with posturing (Figure 19), urinating, and defecating whereby the latter functions, too, can appear ritualized. The ceremonial penial swing, with the penis fully extruded, erect, and enlarged, is quite different from the mere protruding of the pale, wrinkled, and small penis during the act of urinating and defecating when the male is not sexually motivated.

Quite regularly before the first rains come, the males, either with their mates or alone, select or re-establish their breeding territories and choose prospective nest-sites, usually remote from the communal grounds and from the water-sites frequented by so many animals. The most common reproductive unit observed so far in the South West African veld consists of the polygamous family of three hens—i.e., one major hen and two minor hens, mated to one cock (Figure 20). Other marriage bonds also exist; more than three hens can be associated with one cock, and we also observed monogamy in the small Ombu population where adult females were rare in 1964. Judged by the size of a clutch of 43 eggs, five hens must have laid in one nest on Etosha Pan. In large populations our counts of sexually mature birds usually approximated a 1:3 ratio of cocks and hens, and we are inclined to call this a "balanced" population under the local natural conditions existing at the present time. Again, the Ostrich's ability to adjust its mode of marriage bond, according to momentary populational conditions and needs, seems to be of significant adaptive value for the species.

On their nesting grounds the males utter their "booming" calls by which rivals establish their territories, and which can be heard most frequently during the early morning hours and from the late afternoon until as late as midnight, and rarely all night at irregular intervals. The male's mostly four-syllabled *boo boo boooh'hoo,* which one may well call a courtship song, proved to be part of the symbolic nest-site display between male and female during their precopulatory courtship. This is a most spectacular show; we saw it initiated by the male and usually given in remote areas where the cock with one mate is temporarily secluded from the group. Initiating the ceremony, male and female wander about and become highly synchronized in their feeding activities, their heads usually close together near the ground and every move and turn made in unison. Their feeding, however, is performed in a very nervous fashion, very rapidly and superficially, quite characteristic of a symbolic or ritualized act. During preliminary stages of their courtship period, the ceremony easily breaks off at this level of performance and the pair begin to graze. When the courtship advances to higher levels of excitement, the two birds walk toward and around an area chosen for the symbolic nest-site display by the male. He throws his wings up in an alternating rhythm of right-left, flashing his white wing feathers. Suddenly he drops to the ground, begins nesting symbolically in a very exaggerated manner whirling dust when his wings sweep the ground. At the same time he twists his neck in a way that resembles a continuous "corkscrew" action. During this performance the cock often repeats his courtship song, while the hen walks in circles either around him or close to him. As she walks with a slow, measured gait, she assumes her typical precopulatory posture, holding her head low, wings curved and pointing down, and her tail drooping. Upon her intention to squat, the cock jumps up and runs over to her, flagging with his wings; the hen drops to the ground, and copulation takes place.

The Nest, Eggs, and Incubation

The Ostriches, primarily the males but also females, mold and scrape their often walled nests—usually measuring about three meters in diameter—in dry sandy river beds and other sandy spots (Figures 21, 22, and 23). Several pathways may lead to and away for a short distance from most nests. Otherwise Ostriches make hardly any trails as do other animals. But on the bare Etosha Pan we saw Ostriches repeatedly piloting their course toward distinct distant landmarks, thereby leaving a more and more pronounced trail behind. When going to and from the water, they regularly like to use the trails made by oryx gazelles, Burchell's zebras (*Equus burchelli*), and other animals. One nest with a successful brood was even located close to a most frequented trail of the mountain zebra (*Equus zebra hartmannae*). But when grazing, the Ostriches commonly swarm out according to the typical pattern of a flock of birds.

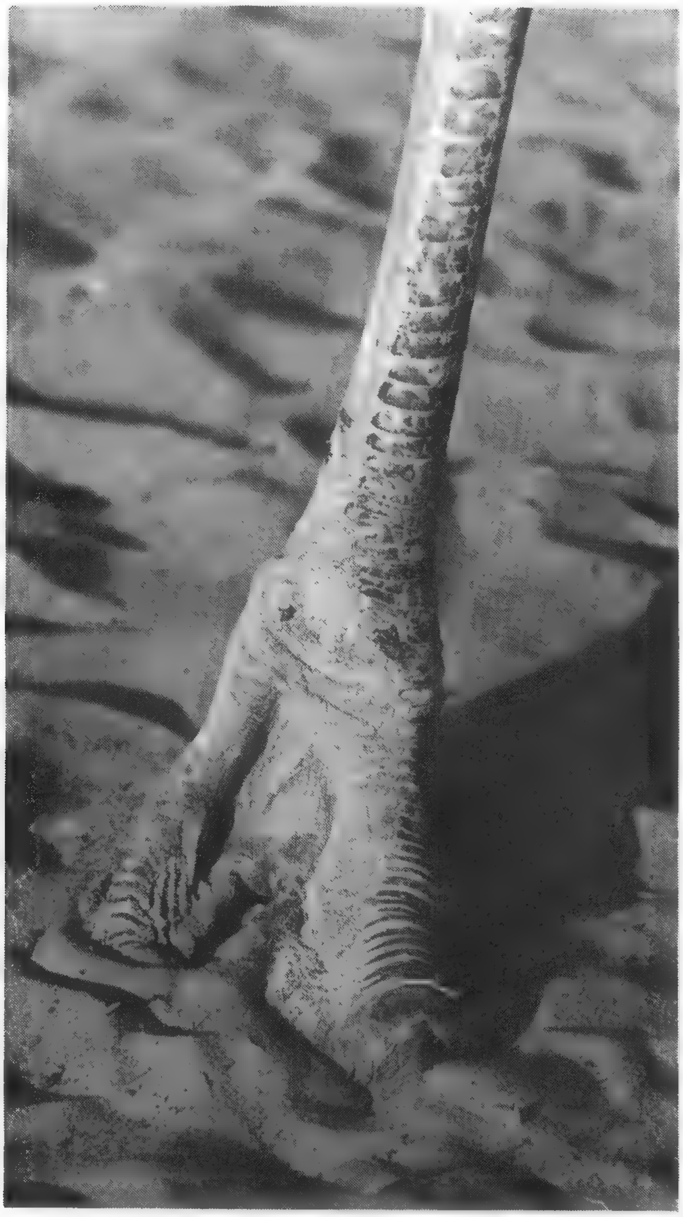


Figure 14. Right foot and shin with black scuta of an adult hen at the beginning of her reproductive cycle. Erindi Ura, Omaheke, 2 August.

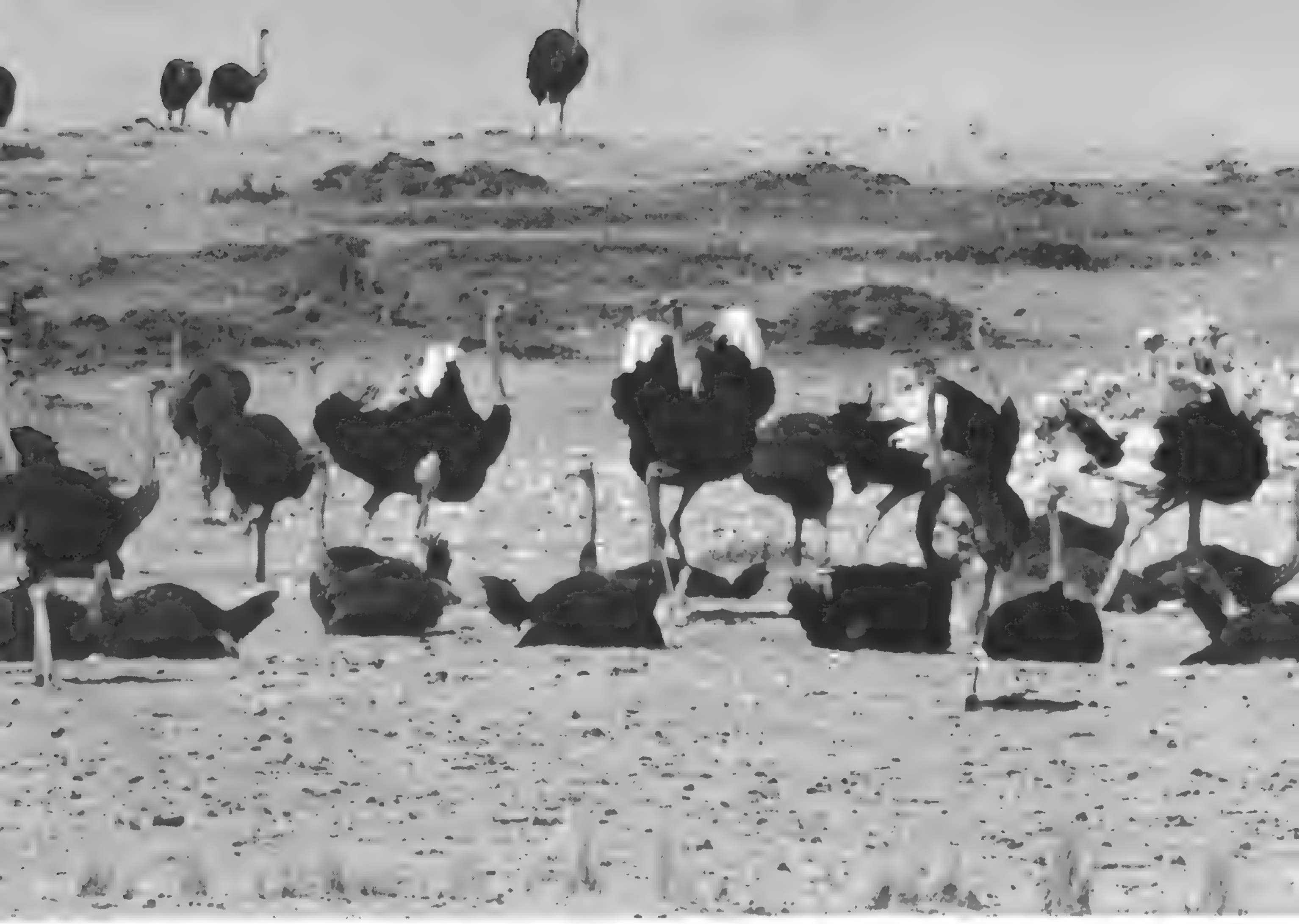
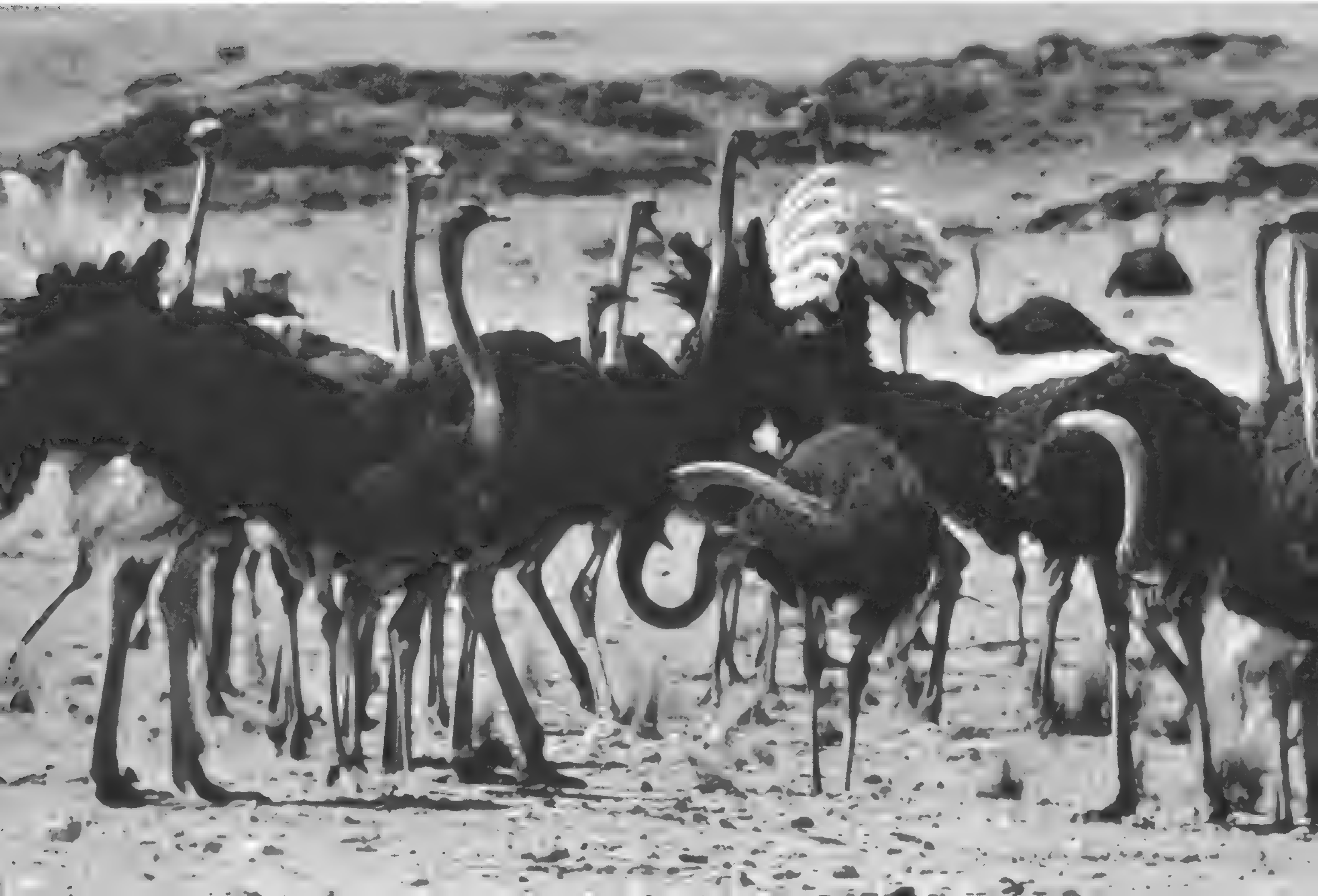


Figure 15 *(above)*. Adult male Ostriches engage in threat displays. The sudden attack by the male on the left is met by the equally strong cock holding both wings high in defense and uttering threat notes. The display triggers a "chain-reaction" that makes the adjacent adult male attack the maturing male to the right. Adult and maturing birds, still on the ground, become affected by the starting tumult, call excitedly, and lift their tails. Hotsas, 19 September.

Figure 16 *(below)*. Beginning of the reproductive cycle, continued. Fighting between adult and maturing males from different flocks. Hotsas, 14 September.



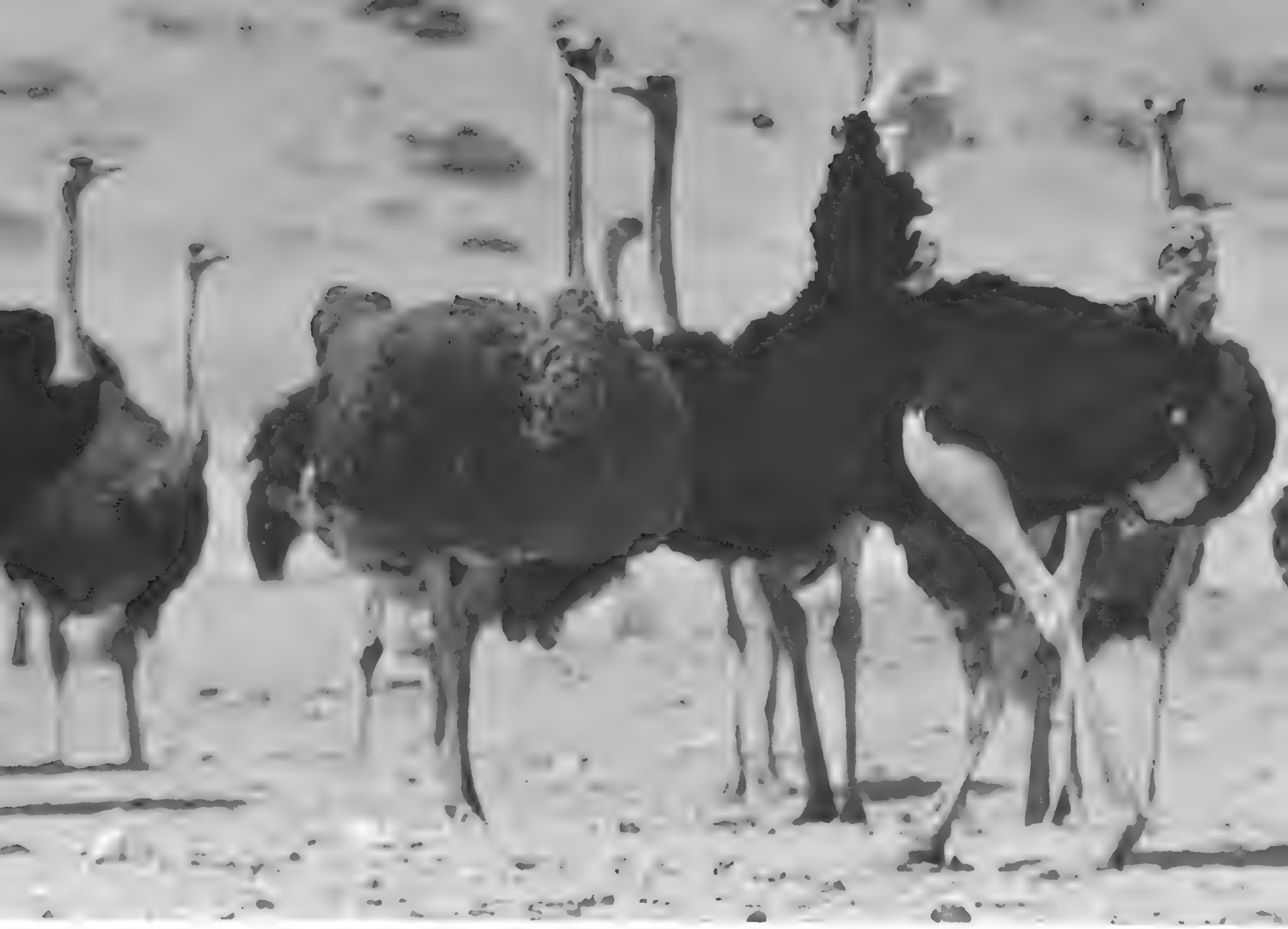
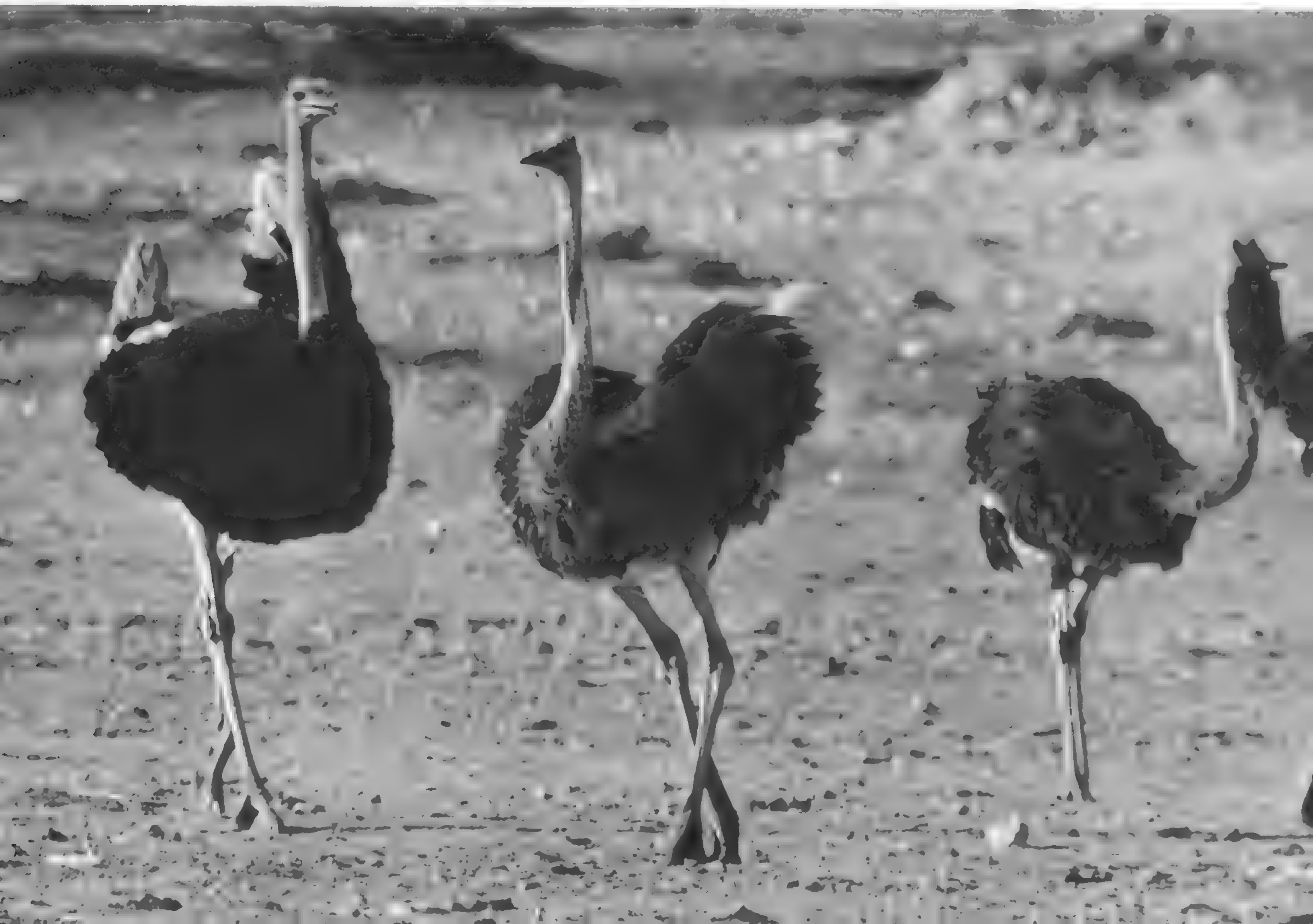


Figure 17 *(above)*. A sexually motivated adult male Ostrich approaches an adult hen while "sweeping" his wings and pointing his tail upward. His approach is met with a firm threat; the hen, with hissing sounds, indicates her disinterest in the cock. Hotsas, 9 September.

Figure 18 *(below)*. A sexually motivated adult male chases yearling which he subsequently kicks. Hotsas, 24 July.



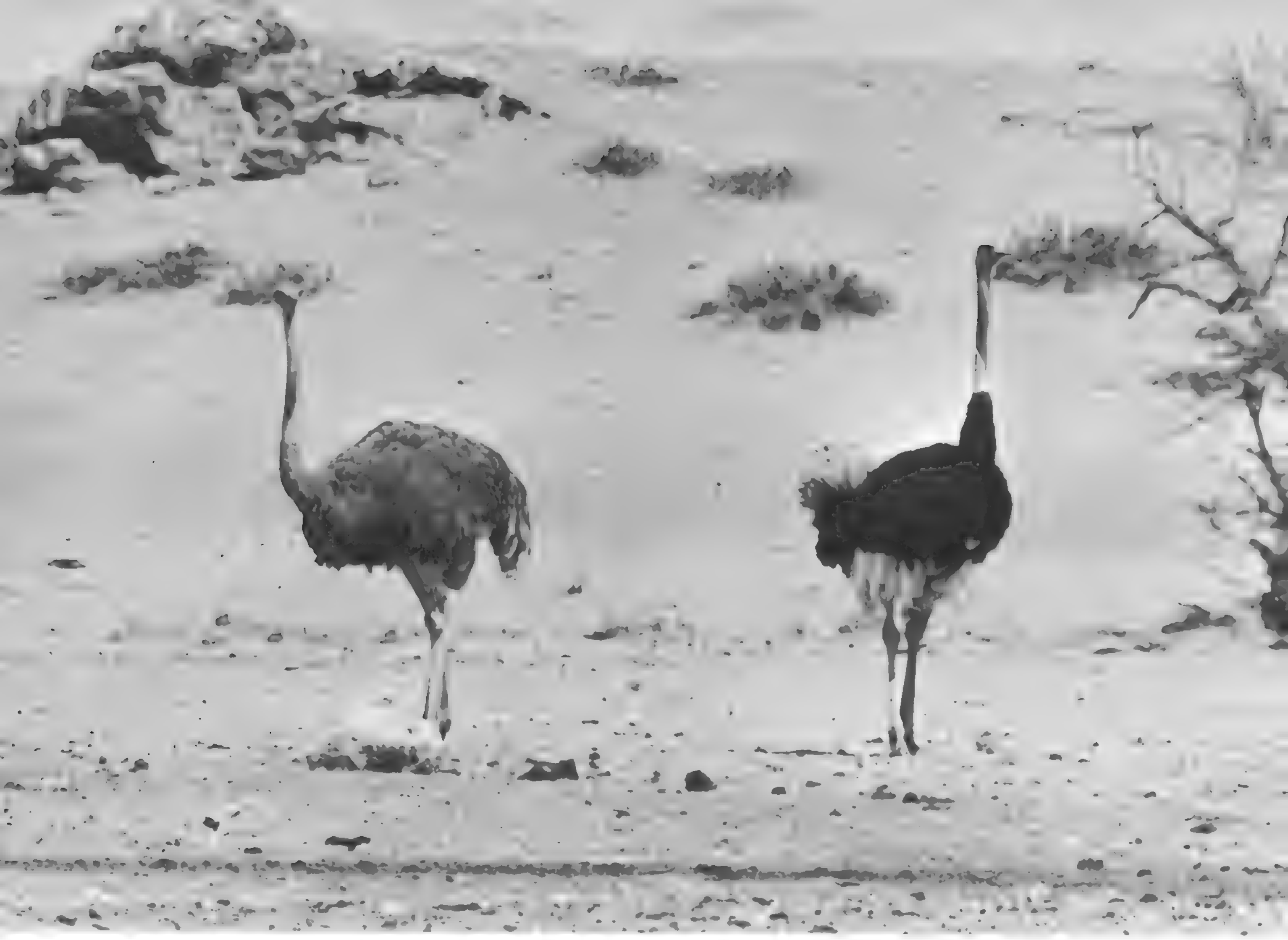
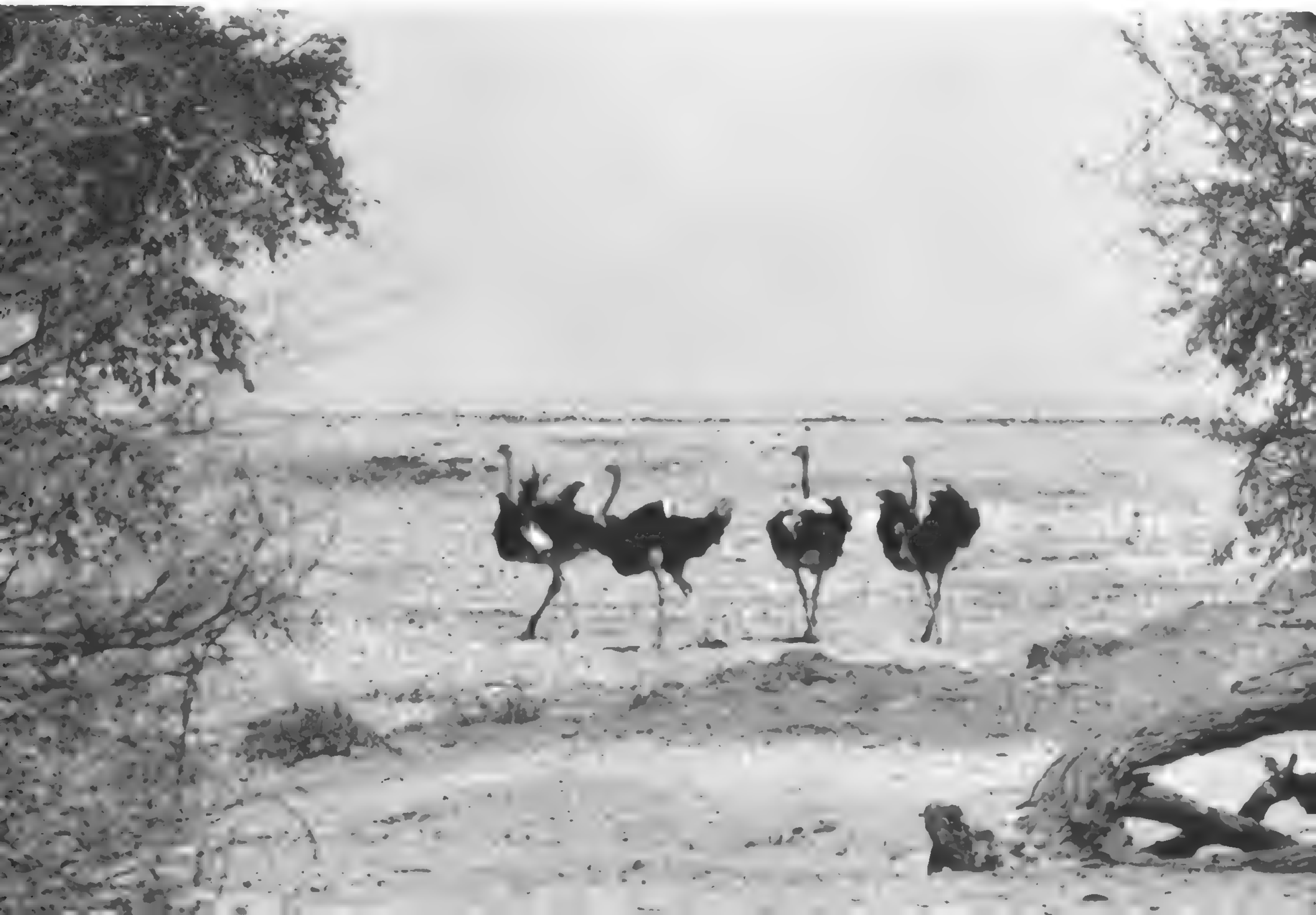


Figure 19 *(above)*. An adult male Ostrich posturing and giving his penial display in front of his mate. Hotsas, 14 September.

Figure 20 *(below)*. Adult male with his three mates, all four highly motivated sexually. The cock separates one hen from the others for temporary isolation initiating precopulatory courtship. Hotsas, 9 September.



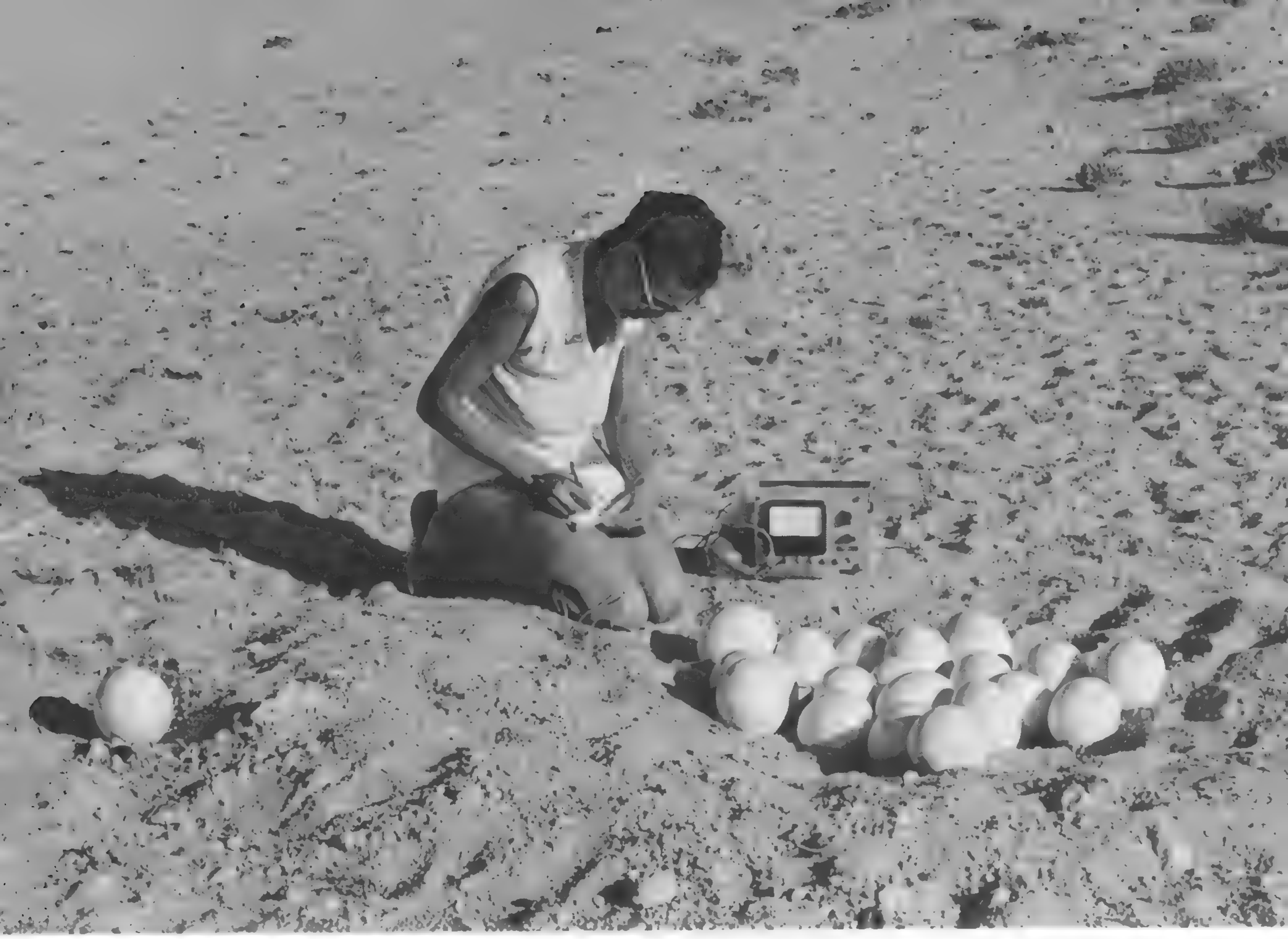
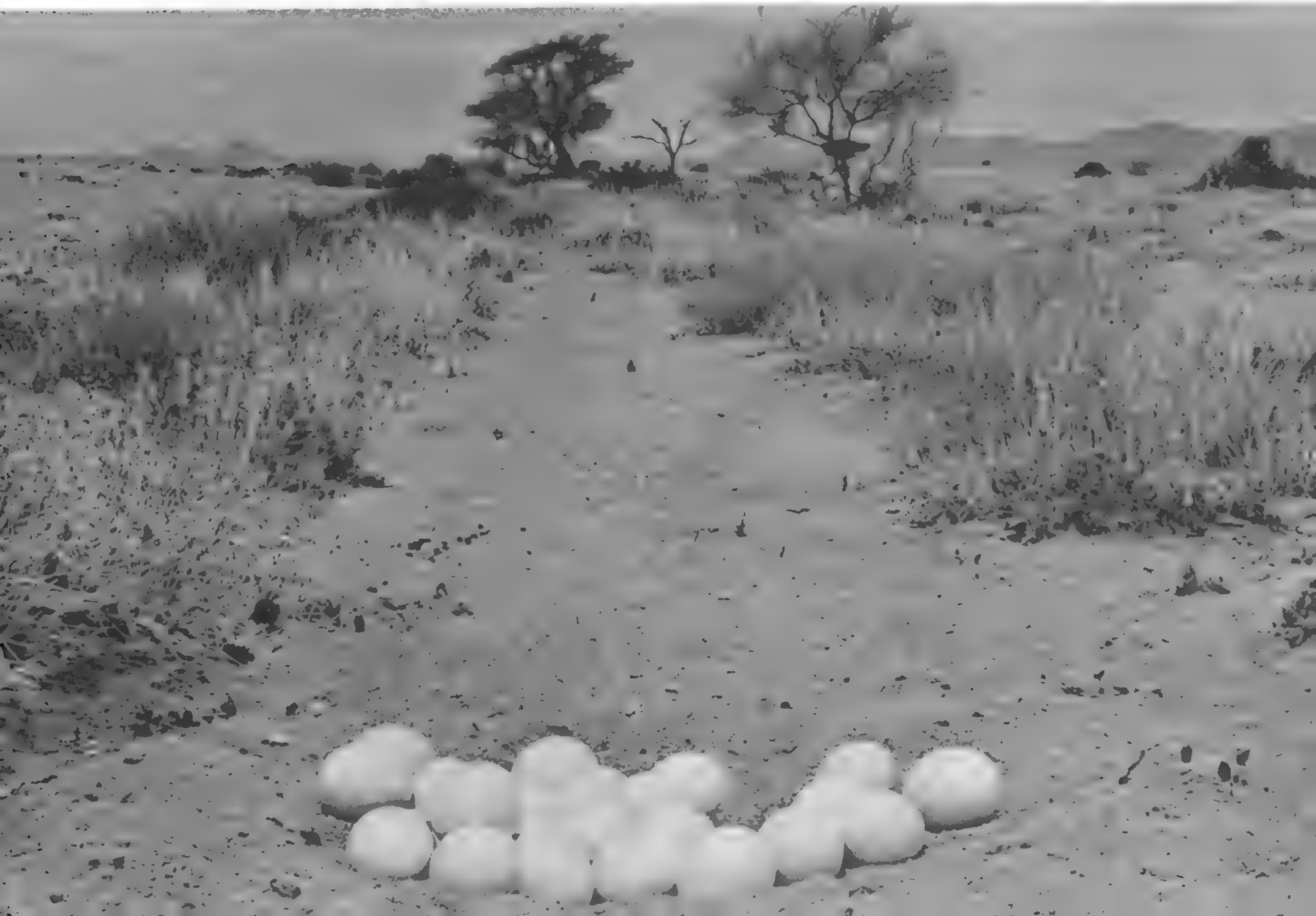


Figure 21 *(above)*. Mrs. Sauer records the egg, sand, and air temperatures in an Ostrich nest (Tinkas Nest 2). The "scatter" egg outside the nest wall was laid where it rests and was never incubated. Tinkas Flats in Game Reserve 3, 27 November.

Figure 22 *(below)*. Hotsas Nest 1 with a clutch of 23 eggs, in a dry river bed. Hotsas, 29 November.



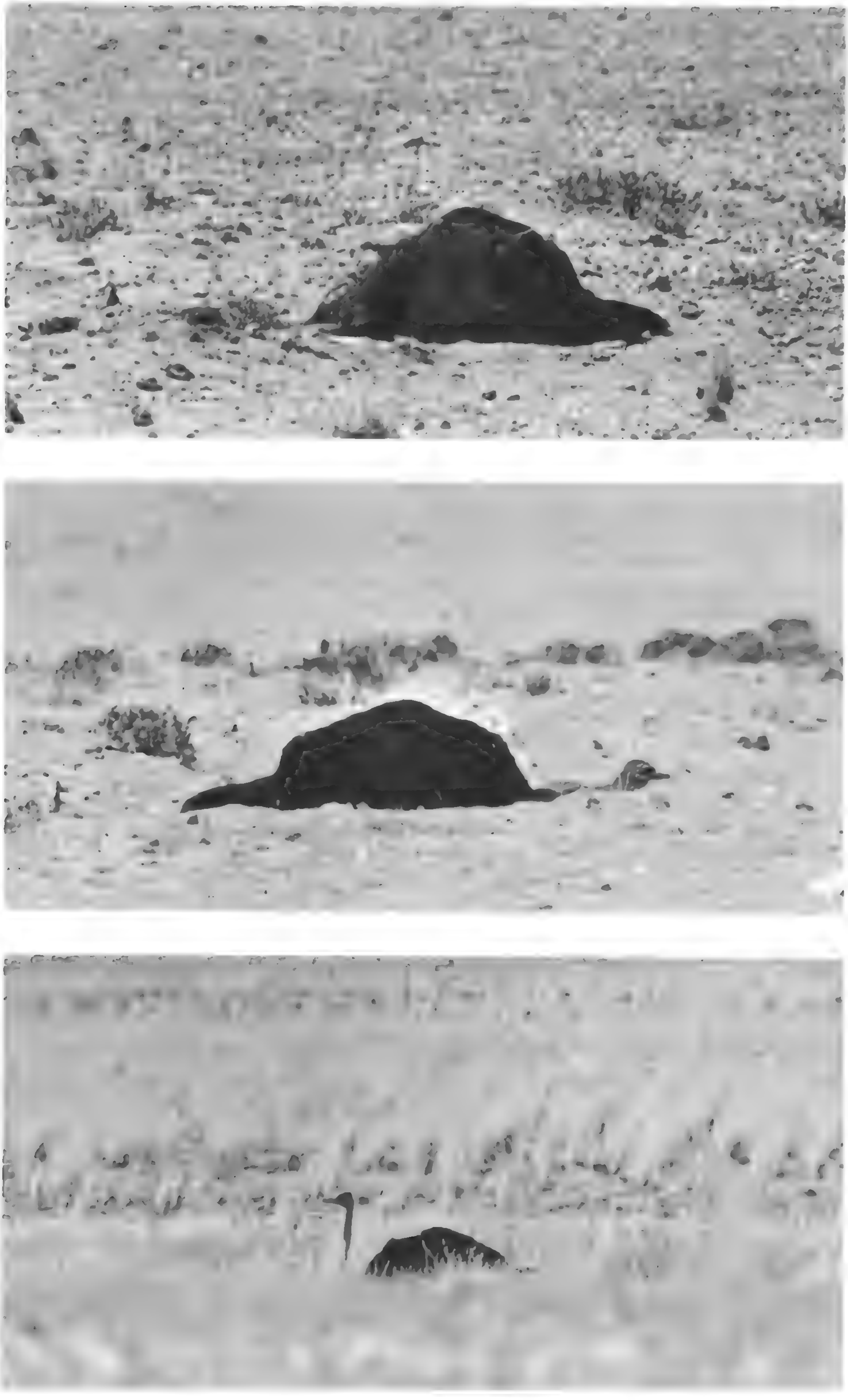


Figure 23. Ostriches on their nests. *Top,* "major hen" incubating a clutch of eggs in Tinkas Nest 2, 5 December. *Middle,* the same hen on the nest on 7 December. *Bottom,* cock incubating on Tinkas Nest 1, 21 November.

The males may guard their still empty nest-sites before the females become interested in them, and before the first booming can be heard. We found a very strong nest-site tenacity in places where nesting had not been disturbed, and sets of older and older shell fragments in single nests indicated that the same nests had been used year after year. September and October, sometimes even August, are the months during which most of the egg-laying takes place. In the nests under control, the eggs were laid mostly during the afternoon and early evening of every other day. The weights of the fresh eggs varied from 755 to 1,618 grams, the low value referring to a first egg of a newly matured hen.

During our two-year study, most clutch-sizes ranged from 16 to 23 eggs, with the maximum contributions of single females to the clutches not exceeding 8 eggs. Newly matured minor hens did lay as few as 3 and 4 eggs in a nest. We believe that the much larger clutches reported from single females in captivity result from the provision of more ample and overly rich food; in part, we may consider it an attribute of their domestication. The limited numbers of eggs of the wild Ostriches in the South West African veld seems to reflect a distinct correlation between clutch size, age of the hen, population density, availability of food and water, and possibly other environmental factors.

The birds guard their eggs prior to incubation, and on the average the clutch is completed within two weeks or a few more days depending on the maximum number of eggs from a single hen, as well as the synchronization of the egg-laying of the minor hens with that of the major hen. For a specific example, see F. Sauer and E. Sauer (1959).

Each of the adult birds can perform the duty of watching the nest-site from the moment the first egg is laid. At times a guard getting interested in grazing may become inattentive and walk away. As a rule, the cock is the main guard before incubation starts. He may sit some 40 meters, or sometimes less, away in the dry grass or a sandy spot where he performs comfort movements such as preening and dust-bathing; or, every once in a while, he may fall asleep. When getting more active, he may graze slowly up and down nearby, always keeping an eye on the nest. As the number of eggs increases he sometimes may move so close that it becomes difficult for us to tell whether he is actually sitting on the eggs or just shading them with his wings during the hot noon hours.

With the completion of the clutch, incubation starts, and then the eggs are turned and displaced daily. Normally this is done when the incubating adult swivels freely and very inconspicuously on top of its clutch. The use of its beak in turning the eggs seems to be limited to the few minutes once or twice a day when it stands up to rearrange the nest. At times the synchronization of the hens' egg-laying causes a problem to get all the eggs into the nest. Eggs kicked out of the nest quite incidentally were always left there and not retrieved. We never observed any Ostrich rolling an egg back into the nest even when it was laid just a few centimeters outside.

In 1957, we noticed a strange phenomenon at the nest of one family of three hens and one cock. Toward the end of incubation when the eggs were almost ready to hatch, the birds made two pits at the edge of the nest and rolled two of the 19 eggs into them. Although these two isolated eggs were within several days of hatching, they were no longer incubated. Our controls indicated that they contained the most advanced embryos of the whole clutch. This situation was quite different from one where "scatter" eggs were found outside the nest from the moment they were laid, something that usually occurs at nests which have excessively large clutches and in which several hens try to lay at the same time (Figure 21). Such scatter eggs are not incubated, and sometimes they can be found enormous distances away from any nest where they are laid by hens after exhaustive runs from sources of danger or by hens lacking a mate. We hoped to find other nests in 1964 where the Ostriches might perhaps actively help to synchronize the time of hatching of the whole clutch by isolating the most advanced eggs from the remaining ones. But we made no confirming observation; in most of the nests, hatching dragged on for days. A possible distinction between more or less advanced eggs could be achieved on the basis of the voice contact between parents and chicks which is established before hatching. However, it is more likely that tolerance among several associated hens, stimulated to incubate at the same time, with their individual tensions balanced by social breeding distances, does account for such a phenomenon.

Very infrequently does a major hen permit one or several minor hens to assist incubating the clutch. More often the major hen will drive the minor hens from the nest-site and away from the territory at different times during the reproductive cycle. But a minor hen will try repeatedly to join the family again with little or no success until she gives up her attempts to incubate or even succeeds in "luring" the cock away from his mate and eggs or offspring.

We recorded air, surface, and egg temperatures at every nest-site and found that during most hours of the day, when the temperatures at ground level began soaring above 55° C, the incubation of the Ostriches consisted largely of cooling rather than warming the eggs.

The cocks usually incubate from the late afternoon or evening until the following morning; one of the well-camouflaged hens, in most instances the major hen, sits on the eggs during the remaining daylight hours. Very rarely does one find several hens on the nest at the same time. Numerous and extreme deviations from the normal pattern of incubation do occur, as when a hen or a cock, for example, sits for 24 hours or even longer at a time. These cases, recorded during continuous observations at single nests, provide, sociologically, the most interesting and fascinating study material and account for the extremely complex and complicated society with their "illegal" social affairs on which we shall report elsewhere.

During the incubation periods, centering around 42 days in the Namib study area, we watched continuously some territorial adults over their whole activity cycles from their awakening before sunrise to their nocturnal sleep begun after sunset. In addition, we had night controls that revealed information on their sleeping behavior on and off their nests.

Hatching and Family Life

We studied hatching primarily during the months of November and December when it reached a significant peak. Social contact between the Ostrich chicks and the parents, as well as among the chicks, is already initiated acoustically before hatching. In the still unpipped eggs the chicks utter various social calls, most of them of pleasing musical quality, all recorded on tape with the microphone hidden in the nest under the eggs. These first calls trigger hatching behavior and most likely prepare the parents for the event of the appearance of their offspring. Nevertheless, one male, incubating when the first eggshell broke, was scared off the nest and expressed every sign of alarm when the shell cracked with the usual and very loud sound.

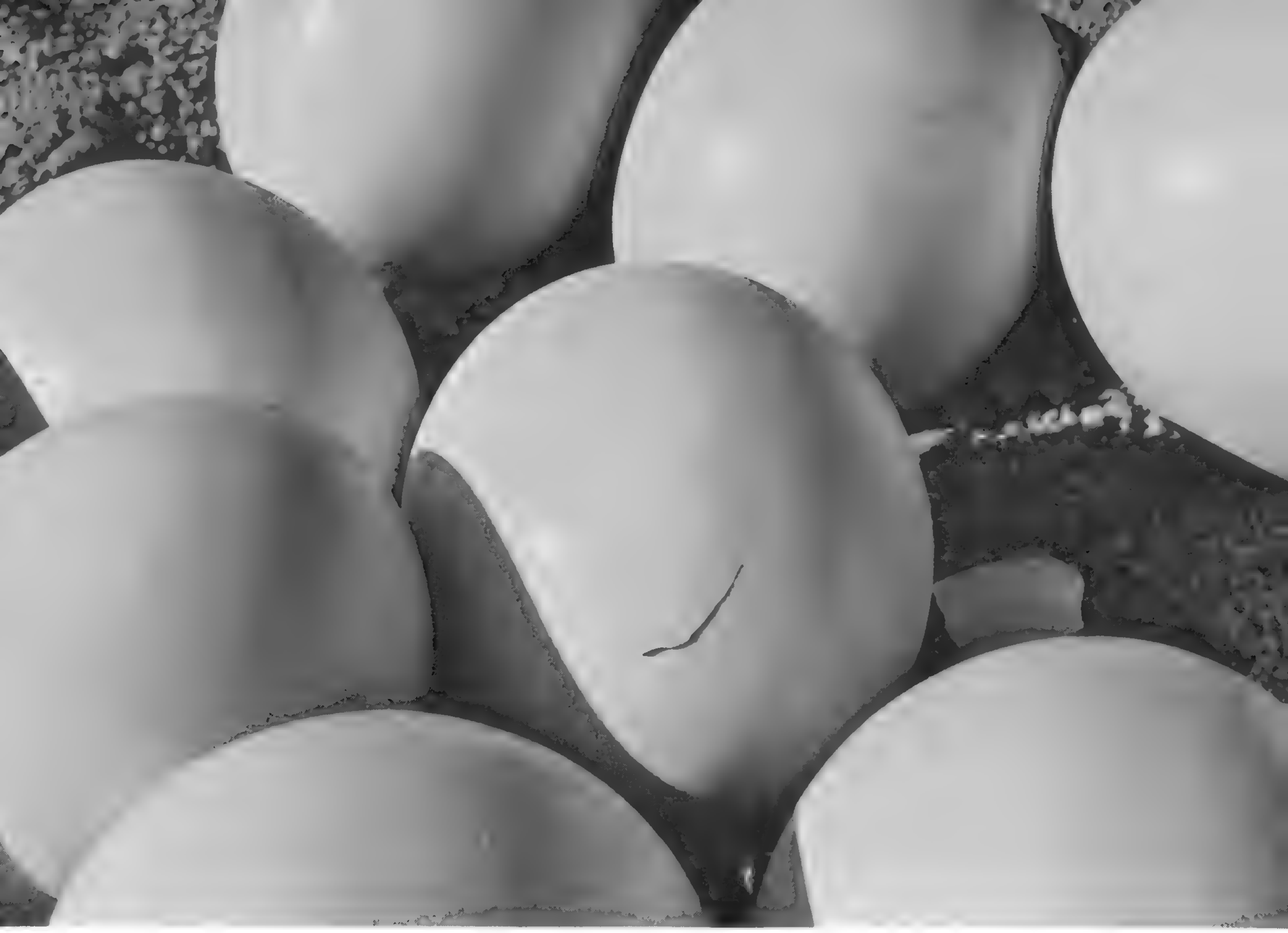
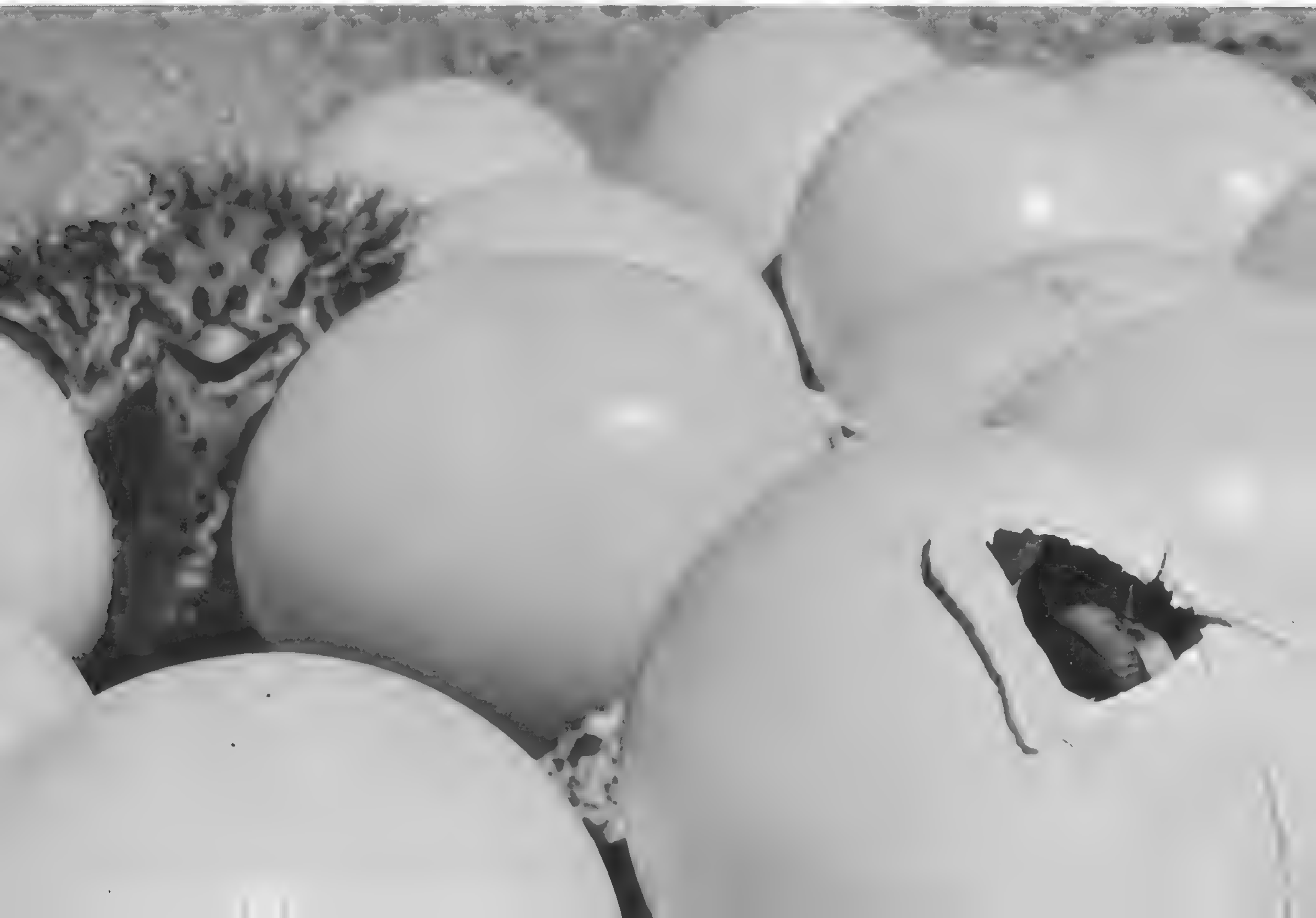


Figure 24 *(above)*. Hatching of an Ostrich egg (middle of picture) begins with a small "window" breaking open. Tinkas Nest 3, 4 December.

Figure 25 *(below)*. Hatching continues with the beak appearing at the open window and a foot (invisible) next to it striking the shell. The hatchling in the rear is panting. Tinkas Nest 2, 11 December.



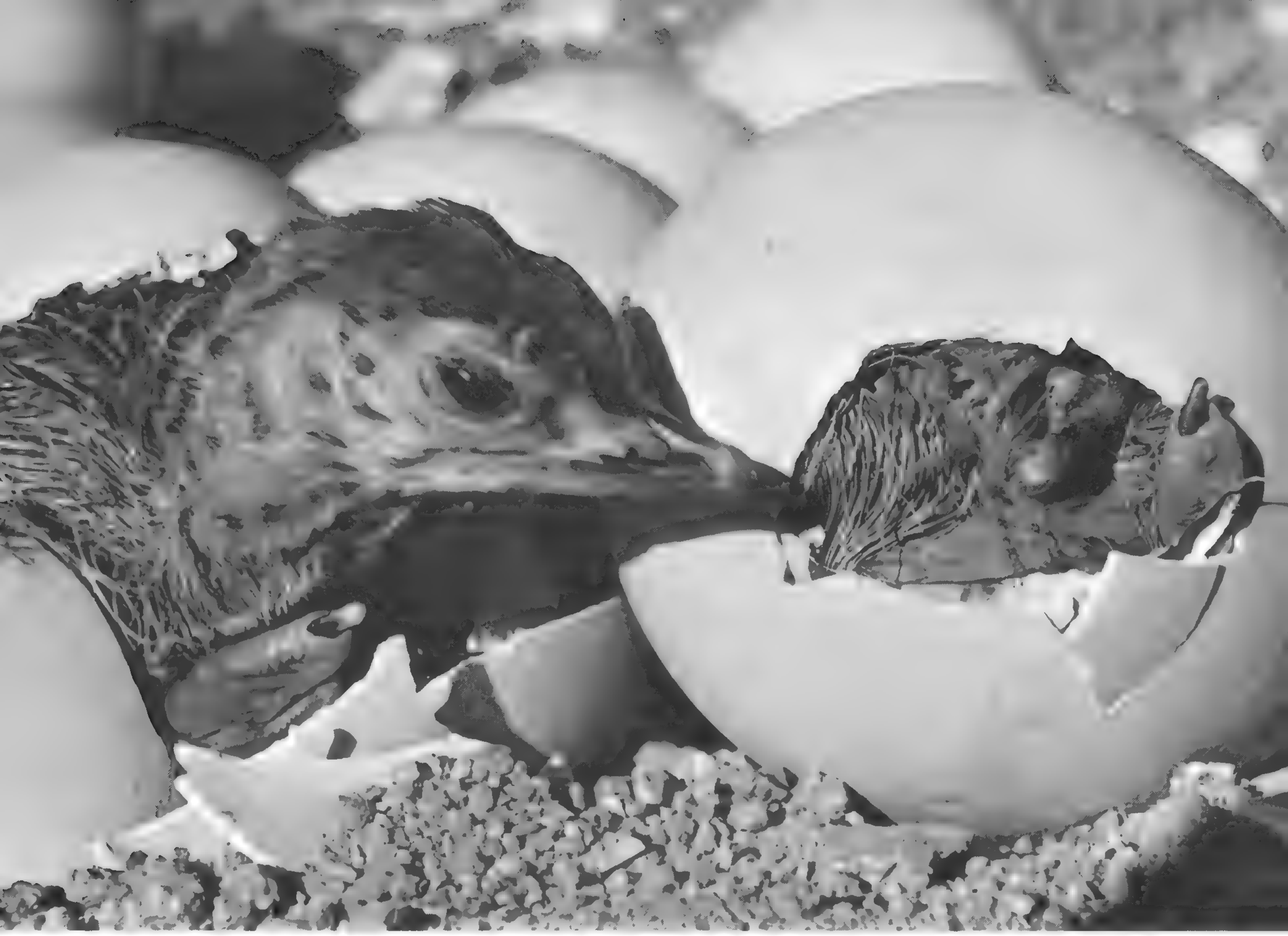
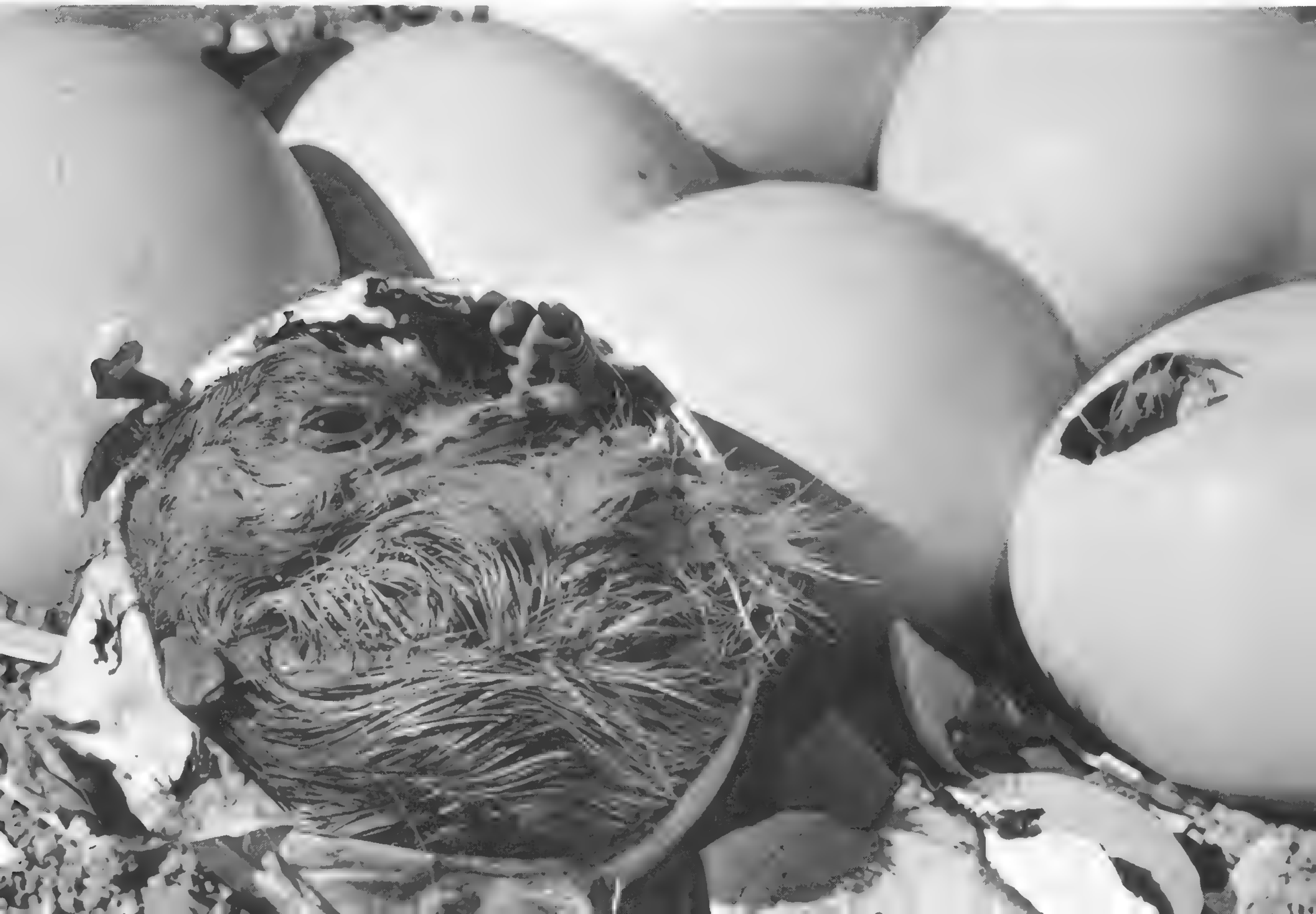


Figure 26 *(above)*. One Ostrich chick at the moment of breaking out of its shell and another enlarging the window with a foot. Tinkas Nest 3, 6 December.

Figure 27 *(below)*. A chick, having a moment ago pushed off a major portion of its shell, remains quiet in a typical hatching position. Its head rests between the feet, with the beak and one foot oriented toward the initial hatching window. Tinkas Nest 3, 7 December.



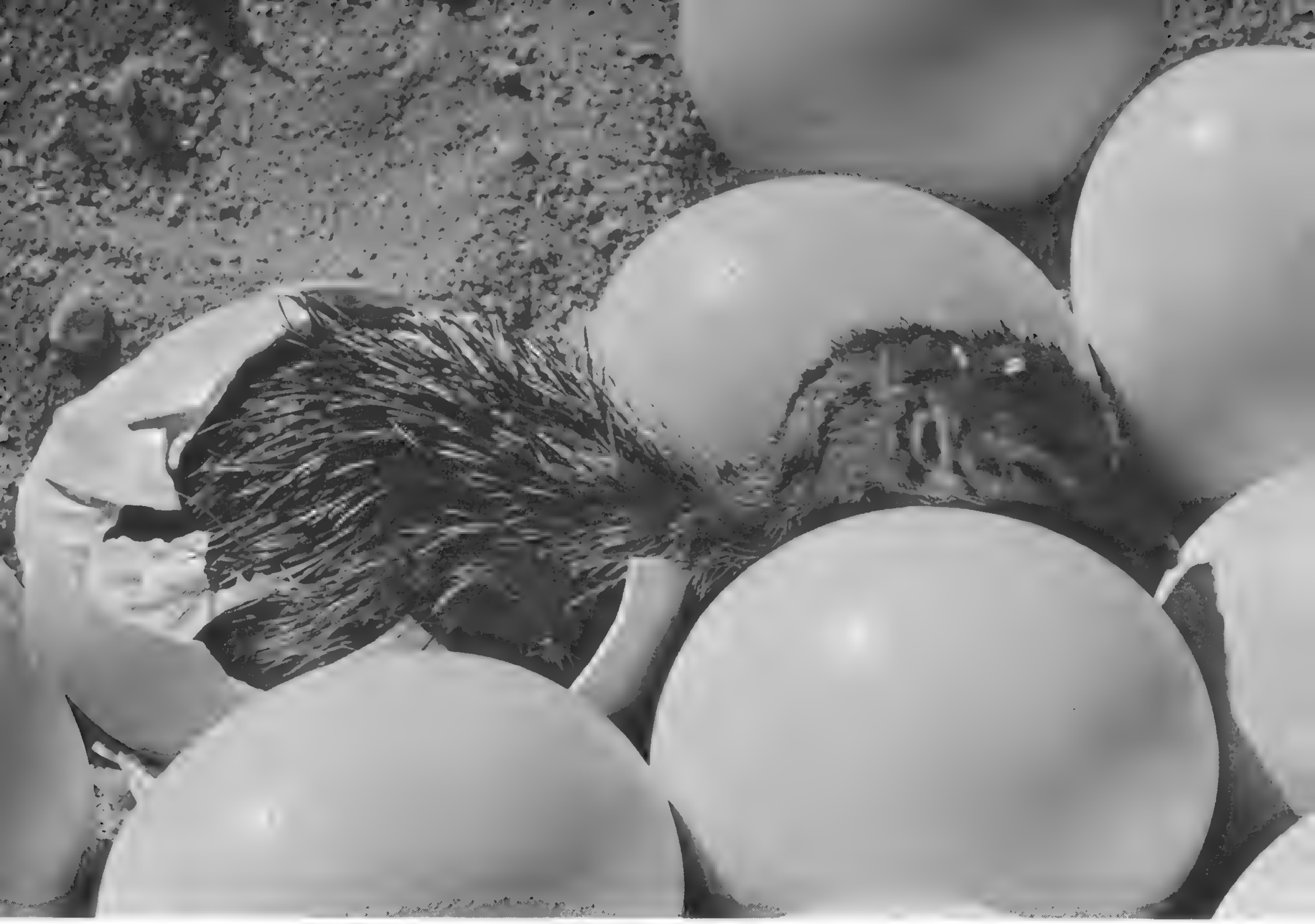


Figure 28 *(above)*. A relaxed Ostrich chick the moment after it jerked its head and neck out of the shell which is breaking to pieces. Parts of the egg membranes stick to the head of the hatchling whose neck is thickened by the heavily developed hatching muscle. Tinkas Nest 1, 22 November.

Figure 29 *(below)*. The major hen Ostrich on Tinkas Nest 2, 12 December, with one chick resting at her neck. Another chick is hidden underneath her tail while she covers two more hatchlings and 16 eggs in the center of the nest. The one egg outside the nest (see Figure 21) is on the right.

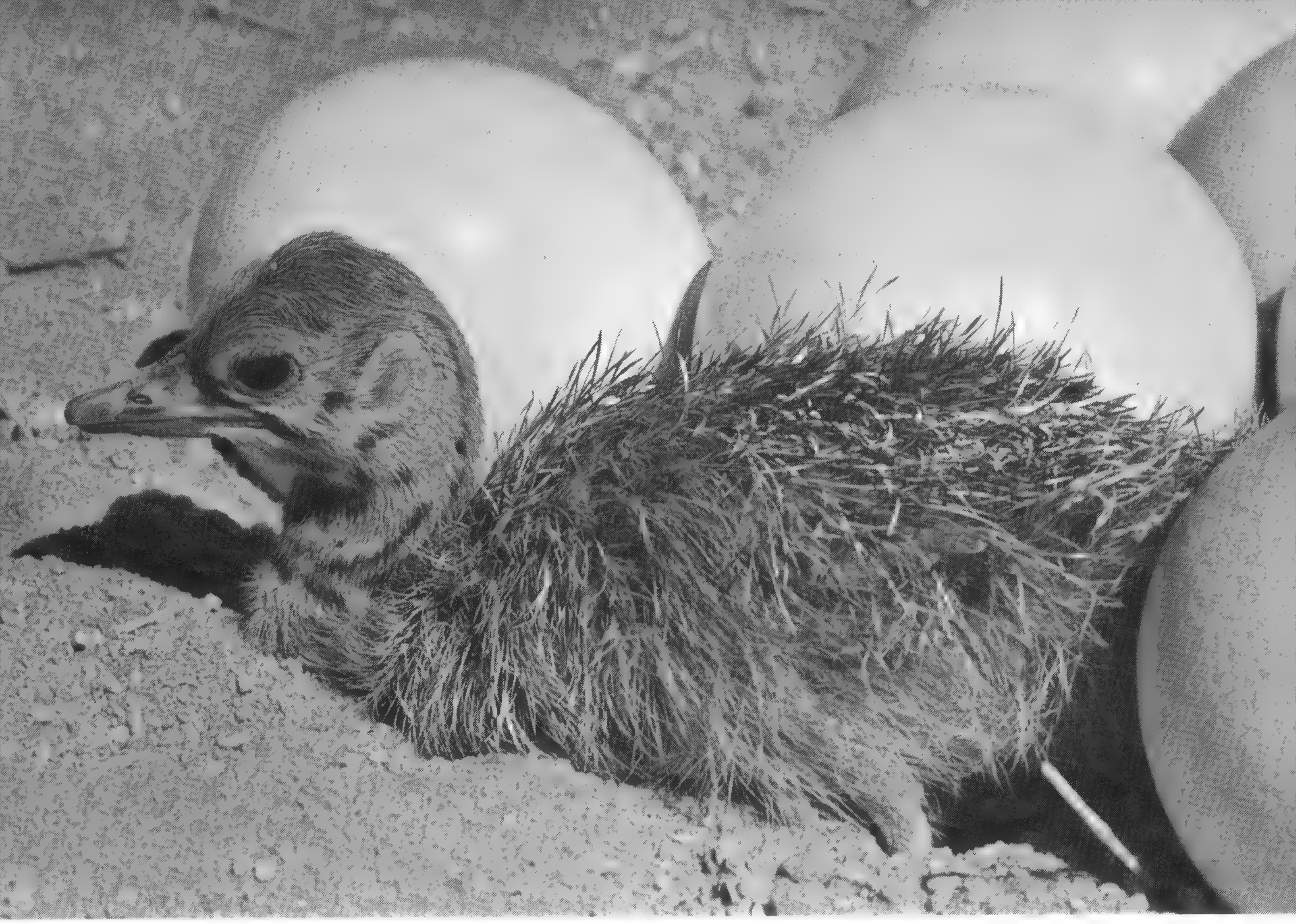


Figure 30. The same Ostrich chick in Figure 28 at the periphery of the nest, 26 November.

The first break of the eggshell, indicated by this sharp cracking sound, seems to be caused by the activity of the strongly developed "hatching muscle" in the neck region. This first break regularly leads to the formation of a small "window" (Figure 24) in which in most cases both the beak and one foot appear with the hatchling frequently oriented in an upside-down position (Figures 25, 26, and 27). Stretching of the body and kicking downward with the foot oriented to this window are the major behavior patterns by which the chicks complete hatching. In nearly all instances it results in a fragmentation of the entire eggshell (Figure 28) and appears to be different from the hatching behavior described as characteristic of many birds. Very rarely does a chick come out of the shell without breaking it into many pieces. The hatching efforts may drag on for hours, even for two days; they are accompanied by various call notes and are interrupted by periods of rest. A "call of triumph" usually announces the moment the chick frees its head from the shell and stretches its neck for the first time (Figure 28).

In the course of two or three days, as more and more hatchlings accumulate in a single nest, they appear from under the adult bird every once in a while (Figure 29), explore the surroundings of the nest (Figures 30, 31, and 32), and swallow small pebbles that aid in grinding the first bits of food. They call when they lose social contact, and fear notes indicate their encounters with the strange new world. At this time social imprinting takes place.

We never observed more than one cock and one hen at a time leading the chicks even when the brood ranged up to 21 in number. But just seeing a pair with chicks in the veld and not having watched the family life of the birds involved can lead to erroneous interpretations. Our uninterrupted observation revealed that one of the pair might even be a step-parent from the very moment the group left the nest-site while the real parent was engaged in courtship activities with another mate.

Parents with fledglings are very shy and very carefully avoid encounters with local predators whose habits and territories they usually know quite well. But when they notice or encounter danger, they quietly steal away or, if this is impossible, they perform an elaborate distraction display (Figures 33 and 34). Spreading and holding the wings low, beating them rapidly, and repeatedly calling *boo,* a male in company of his mate zigzags toward and away from the enemy, presents him with a lateral display and runs to the side, and every once in a while drops to the ground whirling the dust with his wings for a short time before running off again. He is constantly eager to get the attention of the enemy, to separate him from the group, and to lead him away from the well camouflaged chicks. The chicks scatter first and then crouch and remain motionless during the maneuvers of the male. While a displaying male lures an enemy in one direction, the female may suddenly stop her distraction display, call the chicks, and quickly decoy them. In their excitement the chicks frequently give both distress and contact notes.

We observed in the Ostrich's distraction display a number of modifications, depending on the sex of the displaying bird, the presence of one or both parents, individual modes, whether an enemy was in the air or on the ground, or the particular habitat in which the disturbance took place.

Conclusions

This short report on the life of the South African Ostrich, as we studied it in the South West African veld, describes some of our findings. While one may think of the Ostrich as a leftover from a group of relatively primitive birds, we are more inclined to point out the phylogenetic accomplishment in the form of highly complex and very functional structures, abilities, and organizations that reflect the bird's long and successful evolutionary history and made it able to survive to the present day.

The Ostrich appears as a bird highly adapted to live under extreme arid conditions and yet highly able to adjust rapidly to sudden environmental changes and exist in various ecological niches.

At the present time we have not yet analyzed most of our research material. Motor coordinations, such as walking, running, and others; individual behavior patterns, such as feeding, drinking, preening, and dust-bathing; habits of sleeping; and also the various social activities that we recorded and filmed—all these require careful analysis. The process of molting into juvenile, subadult, and adult plumages was noted, as well as various correlations between molt, age, and behavioral changes.

The acoustical communication system, both vocal and "instrumental," exceeds in the number of call notes those of most song birds. The voice-producing organ of the Ostrich, the syrinx, is considered to be so simple and generalized that it lacks tracheo-bronchial muscles and a pessulus and has hardly any specialization of the last tracheal rings. And yet, the vocal sound production of the Ostrich is manifold: it ranges from most complex and melodious phrases of the chick to the mostly hoarse and coarse guttural notes, hissings, and snort calls of the adults. All express specific internal motivation — often minutely differentiated — and all are of social importance, influencing the partner and the behavior of the group significantly. The intra- and interspecific relationships of the Ostrich are also manifold and seem to have reached a level of complexity that equals that of mammals of very advanced social standing.

In the veld of South West Africa we found no other animal as shy and alert as the wild Ostrich. While it occupies a very low rank in the interspecific social rank order of the animals of the veld, many of the animals do rely on its alertness.

In the wild, the Ostrich is vastly different from the tame bird in captivity, especially from the one imprinted on man. Wild creature that it is, it strictly follows the rule "better safe than sorry" and flees from many a harmless animal, such as a flock of Namaqua Sandgrouse (*Pterocles namaqua*), a "joking" Pied Crow, or even a single Ostrich that seeks contact with the herd in a quick run. According to an old proverb, the Ostrich possesses a small brain and little intelligence. However, by being ever alert and ready to run, by using keen eyes and sensitive ears, and, in addition, by taking protracted safety precautions that may result in an unbelievable slowness when it encounters a new and strange situation, the Ostrich has managed to survive to the present day—but only in areas where man has not cut the thread of its life.

Summary

In the years of 1957 and 1958, and extensively in 1964, we studied the South African Ostrich (*Struthio camelus australis*) in various habitats of South West Africa.

The Ostriches are well adapted to live in the arid veld and, at the same time, are highly adaptable and able to occupy diverse ecological niches with extremely different sources of food and water supplies. The Ostriches also respond quickly to untimely and sporadic climatic and other environmental changes, and they flourish in the unpredictable and fluctuating South West African climate as successful opportunist breeders. Following the normal annual cycle of one cold-dry and one warm-rainy season, the Ostrich's reproductive activities reach a peak just before the beginning of the rainy season, but some offspring are hatched at any time of the year.

During the dry season the Ostriches are predominantly organized in superfamily units numbering up to large herds of both adult and immature birds of both sexes, and varying greatly in structure. Various social contacts are established through inter-group communication in communal pastures around water holes.

Mating bonds are predominantly polygynous-polygamous, with the most frequent association of one "major hen" with two "minor hens" and one cock in a "balanced" population. Other polygamous mating bonds and also monogamy exist and reflect the Ostrich's ability to adjust its mode of mating bond according to momentary populational conditions and needs.

Availability of sufficient food over a length of time and the social standing of the hens in the community appear to be the major factors which build up the females' reproductive potential and trigger their reproductive activities. This usually coincides with the completion of their molt.

Various prenuptial and precopulatory displays, nest-site selection, and copulatory behavior are briefly mentioned as they are shown by males and females within the herds and during reproductive isolation in their breeding territories far from the communal grounds.

Ostriches make their nests, approximately 3 meters in diameter, in dry sandy river beds or in other sandy spots. Nest-site tenacity is very strong where nesting is successful. The eggs are laid mostly during the afternoon or early evening of every other day; the hens' egg-laying often becomes synchronized.

Egg weights ranged from 755 to 1,618 grams. Most of the clutch sizes varied between 16 to 23 eggs; the extreme of 43 eggs in one nest on Etosha Pan appears to be very exceptional and reflects an "unbalanced" ratio of adult males to females in the population at the time. The maximum contributions of single females to one clutch did not exceed 8 eggs.

Incubation starts when the clutch is complete, and, during the hot daylight hours, is frequently a cooling rather than warming of the eggs. In the Namib Desert, chicks began to hatch after 39 to 42 days of incubation.

In most instances the minor hens are driven from the nest by the major hen as soon as

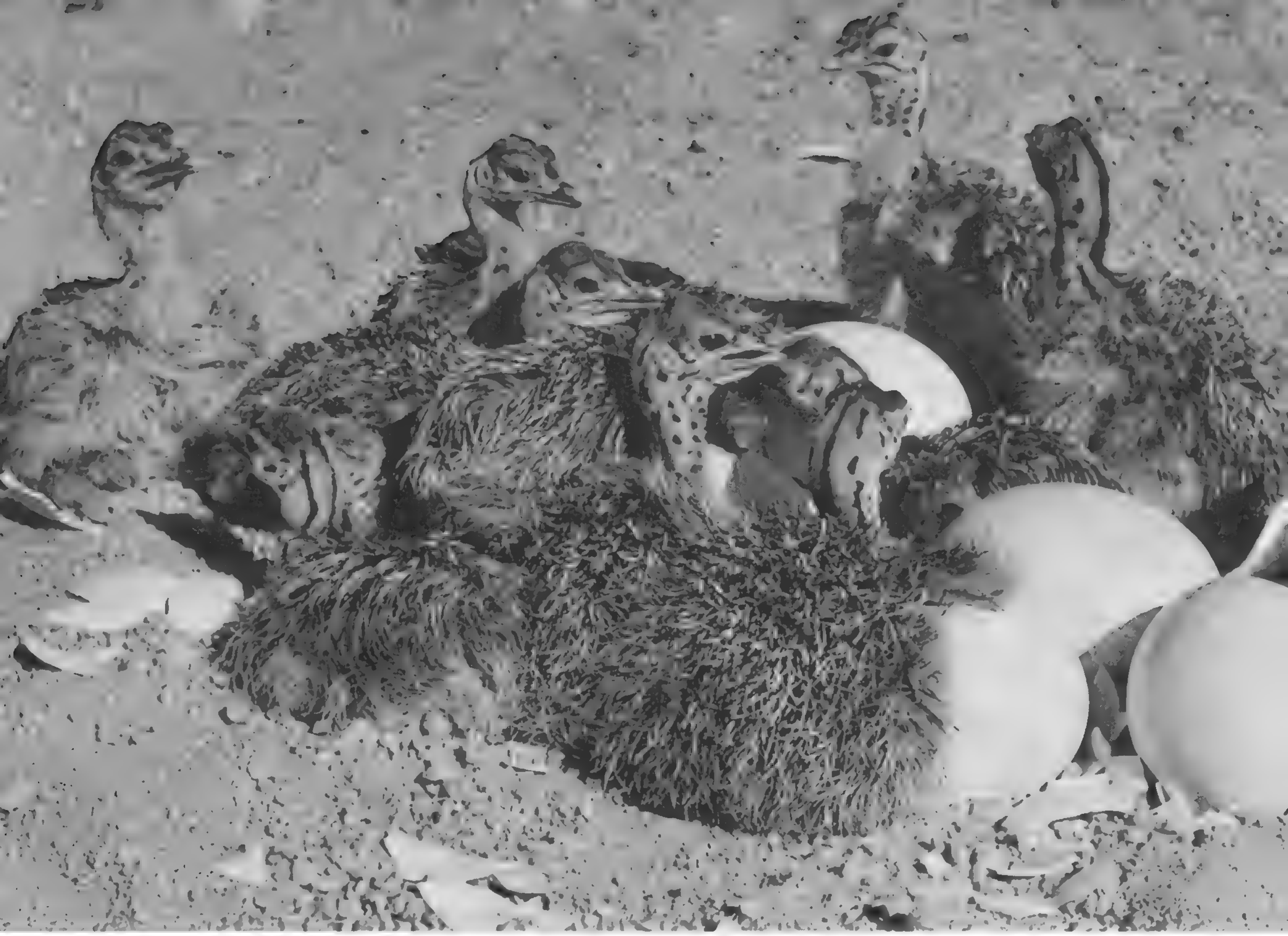
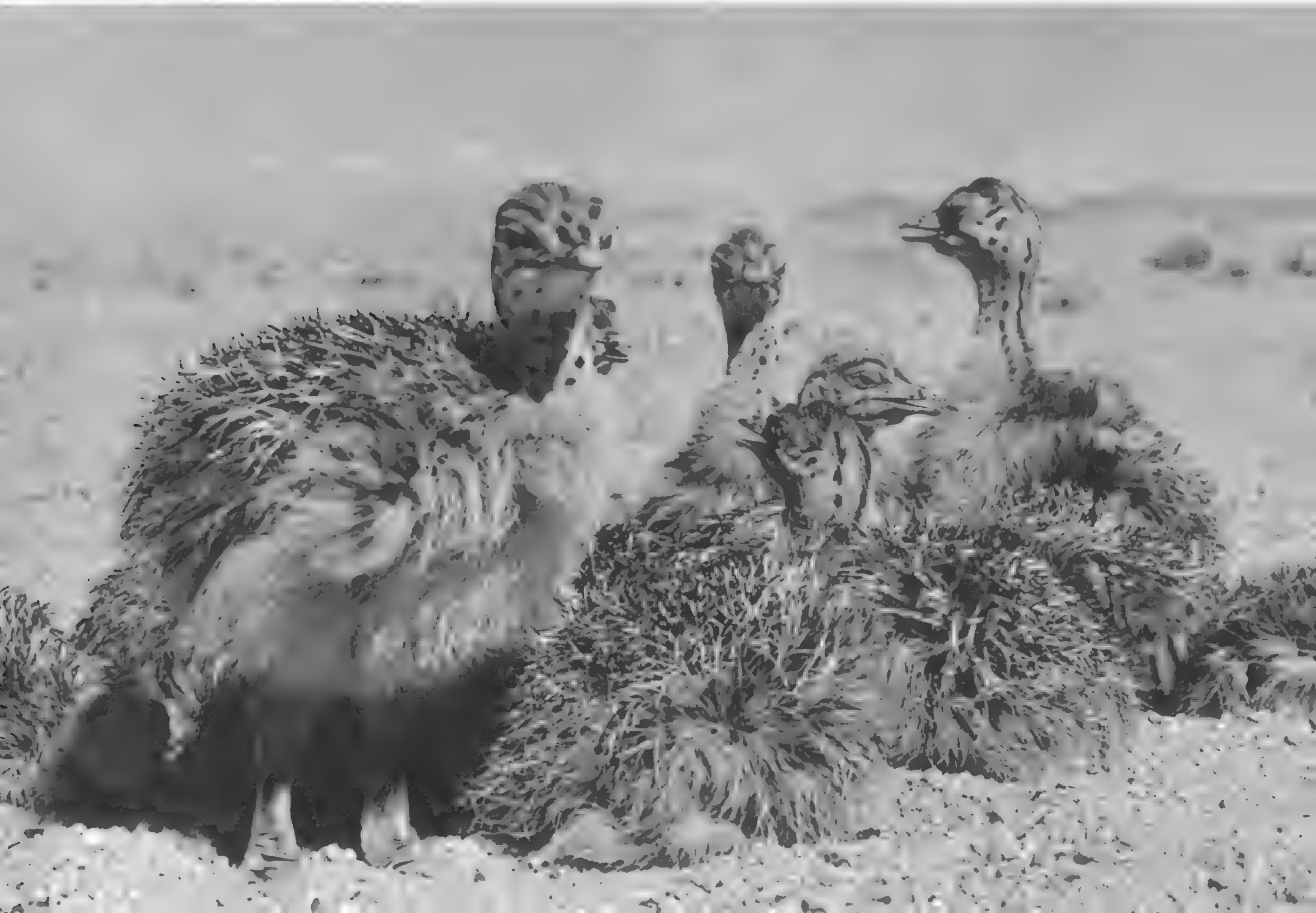


Figure 31 *(above)*. An assembly of Ostrich chicks at the edge of Tinkas Nest 2, 12 December.

Figure 32 *(below)*. Chicks on 13 December from the same nest, resting during their exploratory activities in its immediate neighborhood.



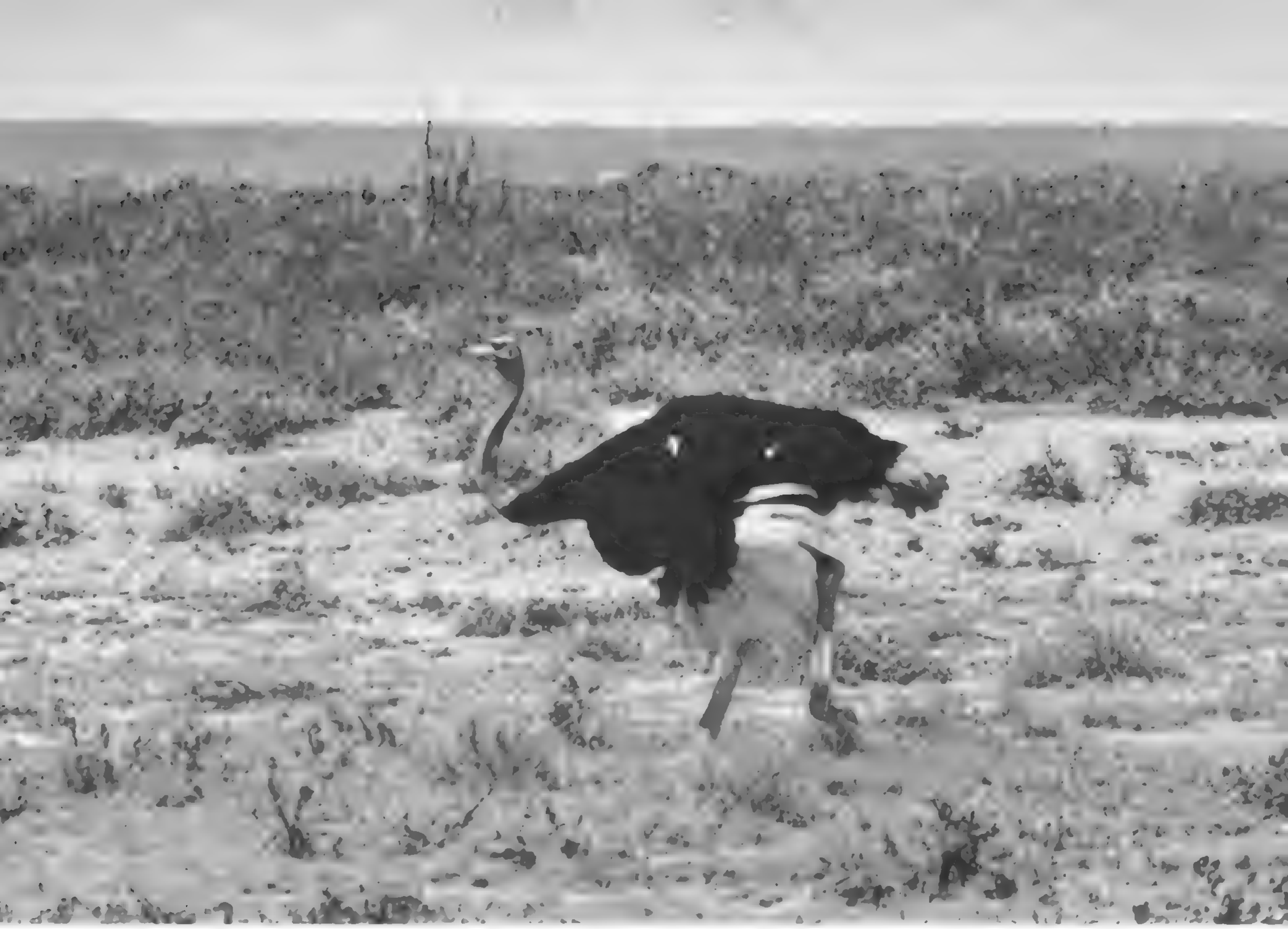
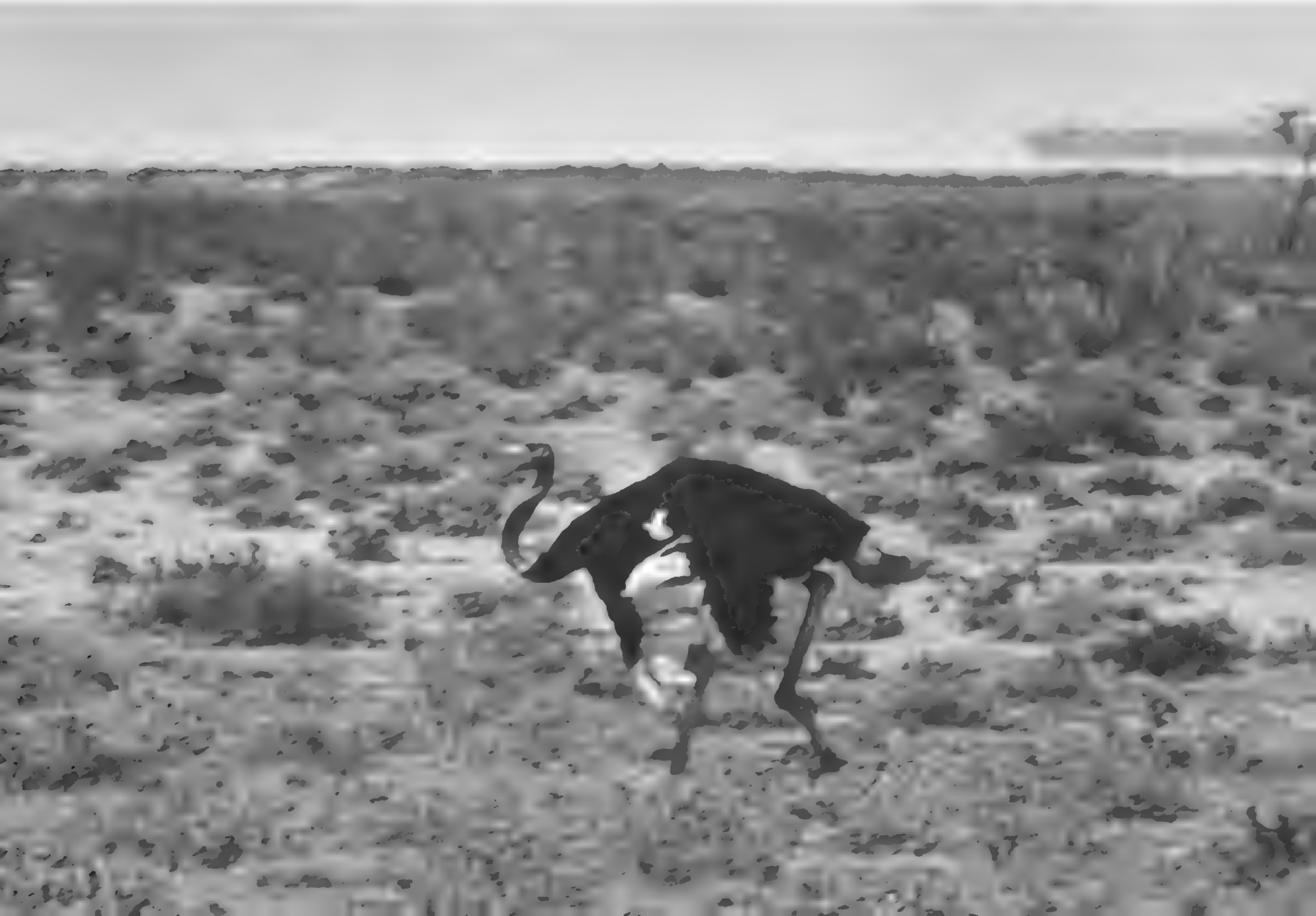


Figure 33 *(above)*. Distraction display of a male Ostrich. Here the cock, spreading and holding his wings low and beating them rapidly, leads away from the hen and chicks, two days after they left the nest on Etosha Pan.

Figure 34 *(below)*. The same cock displaying. During the performance he calls *boo* repeatedly. **Kapupuhedi**. Etosha Game Reserve, 12 November.



egg-laying is completed. In exceptional cases the latter tolerates the presence of one or several minor hens at the nest-site during the period of incubation and permits them to incubate the eggs for certain lengths of time. While the cock usually incubates from the late afternoon or evening until the following morning and the hen during the remaining daylight hours, numerous and extreme deviations from this pattern of incubation do occur.

Social contact between the chicks and the parent birds, as well as among the chicks, is initiated acoustically before hatching. The hatching process commonly begins with the formation of a hatching "window," in which the beak and one foot appear, and results usually in a complete fragmentation of the eggshell.

The major hen and the cock lead the chicks from the nest and remain associated with them for a time usually up to one year or to the beginning of another reproductive cycle. Various exceptions to this rule can be found, and inter-family adoptions of immatures do occur. Parents with chicks perform elaborate distraction displays in moments of danger.

Acknowledgments

This report on our field studies in South West Africa pertains to a research program supported through Grant GB-2167 from the National Science Foundation. In addition, the Graduate School and the Department of Zoology of the University of Florida provided a 1965 Summer Research Fellowship and equipment used in this research.

Zusammenfassung

Der kurze Bericht über den Südafrikanischen Strauss, *Struthio camelus australis*, bezieht sich auf unsere Studien in verschiedenen Biotopen Südwestafrikas, die in den Jahren 1957/58 während einer von der Deutschen Forschungsgemeinschaft finanzierten Expedition eingeleitet und 1964 mit Unterstützung von der National Science Foundation fortgeführt wurden.

Der flugunfähige Laufvogel Strauss ist für ein Leben im trockenen Veld ausgezeichnet angepasst und gleichzeitig fähig, in einer Reihe von ökologischen Nischen mit extrem verschiedenen Nahrungs- und Wasserangeboten zu existieren. Sein rasches Reagieren auf sporadische und oft unzeitgemässe Klimawechsel findet am deutlichsten Ausdruck in seiner Fähigkeit, als Gelegenheitsbrüter jede günstige Fortpflanzungsmöglichkeit zu nützen. Im normalen Wechsel von Trocken- und Regenzeit erreicht die Fortpflanzungskurve einen deutlichen Gipfel unmittelbar vor Beginn der Regenzeit. Bei den lokal typischen, mannigfaltigen Abweichungen des Klimazyklus von der Norm und den Abstufungen des Klimas in verschiedenen Breiten und Längenregionen Südwestafrikas kann man zu jeder Jahreszeit, auch in den kältesten Monaten, Straussennachzucht in kleineren Ausmassen vorfinden.

In der Trockenzeit sind die Strausse überwiegend in gemischten Verbänden vergesellschaftet, die mitunter die Grösse von Herden von 600 und mehr Vögeln beiderlei Geschlechtes und verschiedener Altersstufen erreichen. Die Zusammensetzungen der einzelnen Gruppen variieren sehr. Mannigfaltige soziale Kontakte zwischen Vögeln verschiedener Verbände führen zu neuen sozialen Verbindungen innerhalb der gemeinsamen Weidegründe in der Nähe von Wasserstellen und sind wichtig für die Formierung neuer Familienverbände.

Die Familienstruktur des Strausses ist überwiegend eine Vielehe in Form einer polygynen Polygamie. Die häufigste Verbindung besteht aus einer Haupthenne, zwei Nebenhennen und einem Hahn. In Abhängigkeit von der Struktur der Population treten auch andere Zusammensetzungen polygyner Vielehen und seltener auch Monogamie auf, die für die Anpassung des Strausses an augenblickliche soziale Anforderungen sprechen. Ausreichende Nahrungsvorräte über bestimmte Zeitspannen und die soziale Rangstellung geschlechtsreifer Hennen sind die wichtigsten Faktoren, die deren Fortpflanzungsbereitschaft bestimmen und das Fortpflanzungsverhalten gewöhnlich zu Ende der Mauser aber nicht unbedingt zu einer bestimmten Jahreszeit auslösen.

Eine Reihe von sozialen Verhaltensweisen von Hähnen und Hennen sind kurz angeführt, ebenso die Ablösung der Fortpflanzungsgruppen von den Verbänden und ihre Aufnahme des Balz- und Brutgeschäftes in den Brutrevieren.

Die im Durchmesser etwa 3 Meter messenden Nester werden in sandigen Trockenflussbetten oder in anderen Sandstellen angelegt. Ortstreue ist vielerorts so ausgeprägt, dass die Vögel das gleiche Nest für eine Reihe von Aufzuchten aufsuchen. Die Eier werden jeden zweiten Tag meistens während des späten Nachmittags oder in den frühen Abendstunden gelegt. Häufig synchronisieren die Nebenhennen ihre Eiablagen mit denen der Haupthenne. Eigewichte variierten von 755g, dem ersten Ei einer gerade geschlechtsreifen Henne, bis 1618g. Die Gelegegrössen in den verschiedenen Beobachtungsgebieten schwankten haupt-

sächlich zwischen 16 und 23 Eiern, wobei einzelne Hennen nicht mehr als höchstens acht Eier beisteuerten. Nebenhennen stellten ihr Legegeschäft mitunter schon nach drei und vier Eiern ein. Grössere Gemeinschaftsgelege bis zu 43 Eiern waren in den Beobachtungsgebieten selten.

Das Brutgeschäft beginnt mit dem vollständigen Gelege und dauerte in der Namib im Durchschnitt 42 Tage. In der Hitze des Tages, mit Oberflächentemperaturen über 55°C., vermieden die Strausse mit ihrem Brüten im wesentlichen ein Ueberhitzen und Austrocknen der Eier, sodass ihr Brutverhalten gewissermassen ein Kühlen der Eier darstellt.

Die Nebenhennen werden gewöhnlich nach Abschluss des Legegeschäftes von der Haupthenne vom Nestplatz gescheucht. Nur in seltenen Fällen duldet sie deren Teilnahme am Brutgeschäft für eine gewisse Zeit. In der Regel brüten der Hahn vom Spätnachmittag oder frühen Abend bis zum andern Morgen und die Henne während der verbleibenden Tageszeit, doch weichen die Vögel in zahlreichen Fällen selbst extrem von dieser Norm ab.

Soziale Kontaktnahme zwischen Küken und Eltern, sowie unter den Küken, beginnt mit Stimmfühlungslauten schon vor dem Schlüpfen. Der Schlüpfakt beginnt mit dem Ausbrechen eines "Fensters" in der Eischale, in dem der Schnabel und ein Fuss zu sehen sind. Im Endeffekt führt das Schlüpfen zu einem vollständigen Zerbrechen der Eischale.

Die Haupthenne und der Hahn führen die Küken und verbleiben mit ihnen bis zu einem Jahr oder bis zum Beginn des nächsten Fortpflanzungszyklus. Von dieser Regel gibt es eine Reihe von Ausnahmen; auch kommt es nicht selten zu Adoptionen von immaturen Vögeln. In Gefahrsituation verleiten Altvögel mit Küken den Feind auf verschiedene Weisen, wobei sich Hahn und Henne derart in ihren Bemühungen ergänzen, dass der Hahn den Feind von den Küken wegzuleiten versucht, während die Henne die Küken in Deckung führt. Beide Altvögel zeigen das Verleiten eines Feindes vom Nestplatz auch schon ehe die Küken schlüpfen.

Eine ausführliche Behandlung des Themas ist für eine Monographie vorgesehen.

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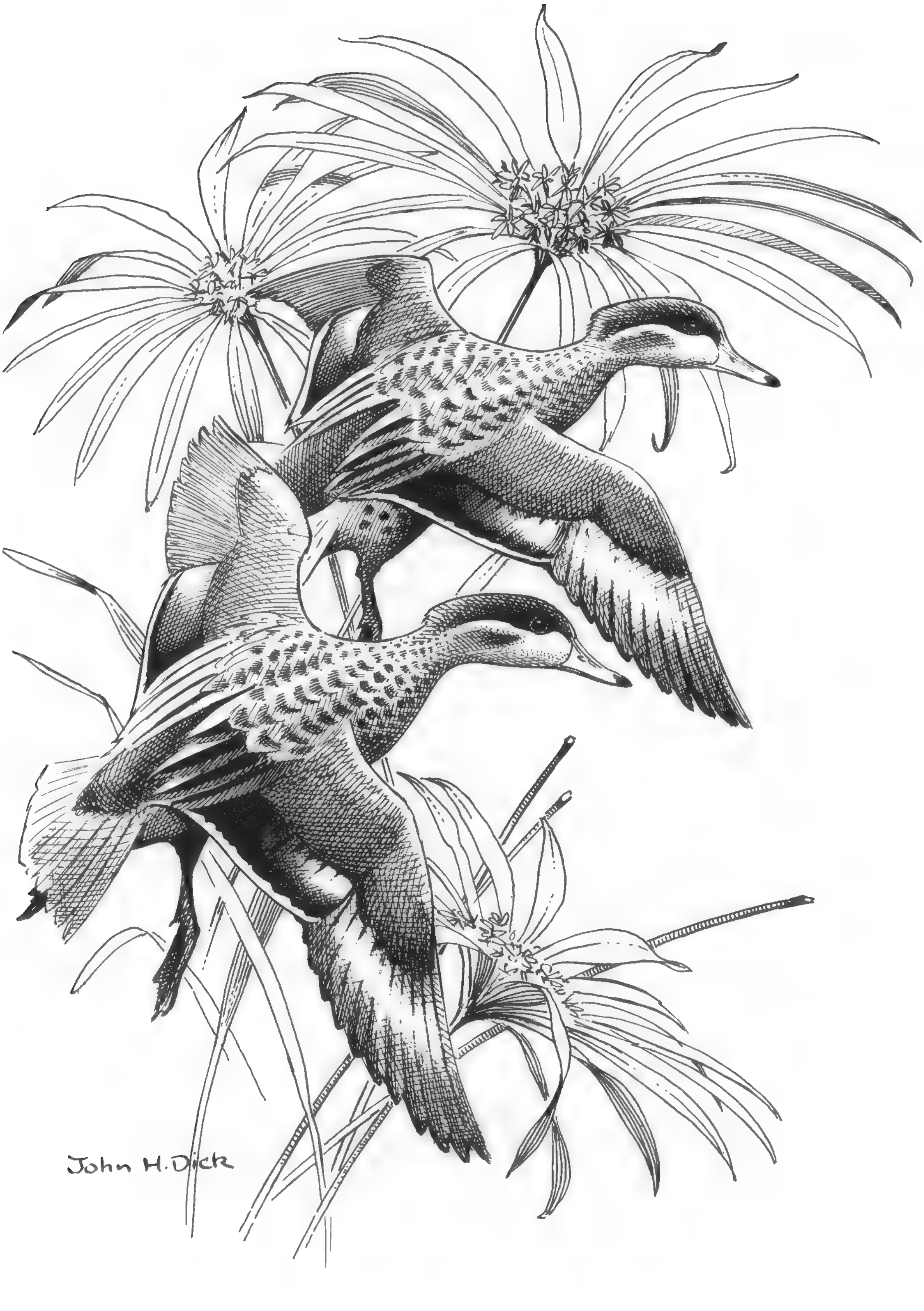

Hottentot Teal, *Anas punctata*. Drawing by John Henry Dick.

SPECULATIONS ON THE ORIGIN OF FEATHERS

Kenneth C. Parkes

A journal entitled *The Living Bird* may seem, at first glance, to be an odd place for a discussion of feathers in relation to a hypothetical train of events which may have happened over 150 million years ago. Yet in the feather we have the one anatomical structure that most clearly differentiates birds from all other animals: no other animal possesses feathers; and all adult birds do (the qualification "adult" is necessary because some birds are wholly featherless when hatched). It must be admitted that we employ some circular reasoning when we define birds as animals possessing feathers; even so, virtually every writer who has discussed the anatomy of *Archaeopteryx,* the earliest known "bird," has stated that, were it not for the fact that *Archaeopteryx* was feathered, this creature would have been classified unhesitatingly as a reptile.

In the conjectures that follow, there is relatively little that is original. Having waded through the morass of contradictory theories and muddy thinking that occurs in so much of the literature on this subject, I have attempted to find what seems to me a logical sequence of possible events in the early evolutionary history of birds. We shall be dealing with pure speculation in that we have no *direct* evidence about the origin of feathers, but I shall try to show why one particular line of thought appears to me to be the most logical, given the presently available information about the earliest creature known to have worn feathers and about the processes of evolution in general.

Archaeopteryx, *the Earliest Known Bird*

As is well known, the fossil record of birds is not particularly good, and it becomes worse the farther back in time we go. But then we come to the late Jurassic Period, some 150 million years ago, and we have *Archaeopteryx,* bearer of the oldest known feathers; *Archaeopteryx,* that strange mosaic of avian and reptilian characters so fully monographed a few years ago by Sir Gavin de Beer of the British Museum (1954). I should like to point out something about *Archaeopteryx* that came as a bit of a shock to me during background reading: In spite of the fact that *Archaeopteryx* is the earliest known bird (or bird-like creature, if you prefer) and that it antedates the next-oldest fossil bird (two bone fragments which have been named *Gallornis*) by some 10 million years, we actually *know* far more about *Archaeopteryx*—what it looked like and how it was put together—than we do about the vast majority of much more recent fossil birds. Of many of the latter we have isolated fragments: the end of a humerus, a coracoid, or perhaps several associated bones *assumed* to have belonged to one kind of bird. We describe the differences between these and the equivalent bones of living species, and we name them as extinct species, genera, or even families and orders. Usually all we can do with these few bones is postulate the appearance of the whole bird and the extent to which it may have resembled familiar living species. Surely the most courageous attempt at such deductions is the series of silhouettes by Peterson (*in* Fisher and Peterson, 1964).

On the other hand, of *Archaeopteryx* we have two amazingly complete impressions in fine-grained lithographic limestone, a third less complete, and an imprint of a single feather which is virtually photographic (Figure 1). The tangible evidence from these excellent fossils allows us to say, as de Beer and others have said, a great deal about *Archaeopteryx*.

One indisputable fact about *Archaeopteryx* provides the core of the present paper: No matter how reptilian it may have been in many of its anatomical characters, it had feathers indistinguishable in any important way from those of living birds. Although the bones of the wing were not fully avian, the feathers themselves and, as far as we can tell, even the general arrangement of the flight feathers corresponded to those of modern birds. This is important to remember—that by the late Jurassic, bird-like reptiles had already "invented" the flight feathers of the wing, and these flight feathers have remained essentially the same, except for relatively minor adaptive variations in shape and proportion, for 150 million years.

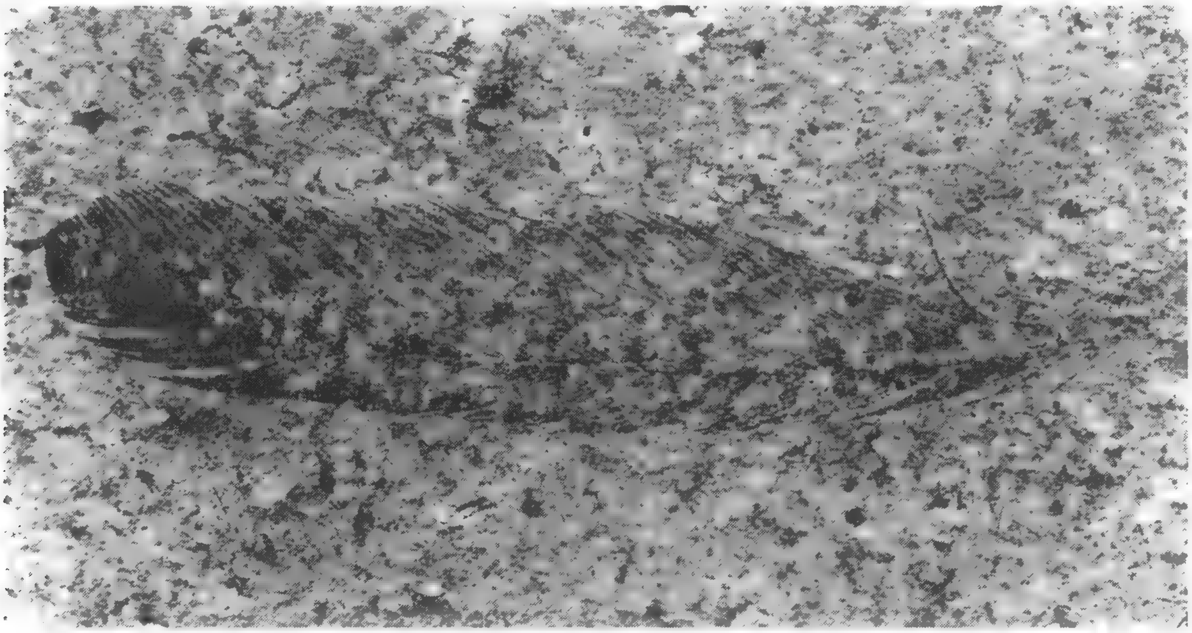

Figure 1. The impression of a single feather of *Archaeopteryx* that was found in a split slab of lithographic limestone and is now in the Berlin Museum. The feather was 69 millimeters long.

The rectrices of *Archaeopteryx* also resembled those of modern birds, but their arrangement was quite different. Instead of being gathered into a single fan at the end of a pygostyle formed of fused caudal vertebrae, the rectrices of *Archaeopteryx* were arranged as a series of pairs on either side of a long, rather lizard-like tail. The specimen in the Berlin Museum shows clearly that contour feathers were also present on the legs and body, but the impressions are too blurred to reveal the shape or structure of individual feathers. In a partial specimen, discovered in 1958 (now in a small museum at Maxberg, near Solnhofen, Bavaria, Germany), there is a strong indication

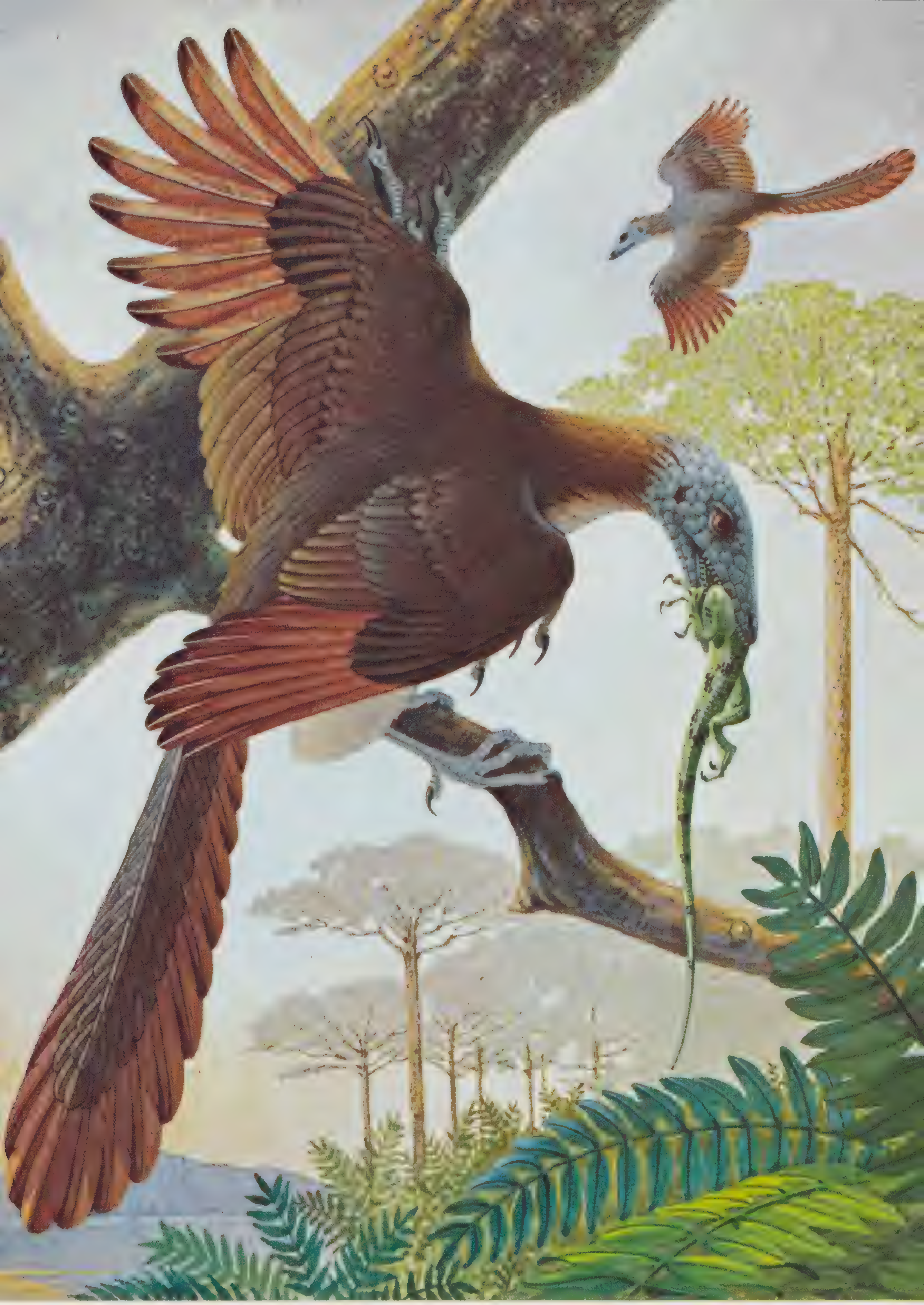

Plate I. A new reconstruction of *Archaeopteryx*. Painting by Rudolf Freund.

that the tibial feathering resembled the "flags" of living hawks (Heller, 1959: 14, plates 4 and 5). However, this specimen was so disarranged before its preservation that the identification of these feather impressions must remain tentative.

How well could *Archaeopteryx* fly, using its typically avian arrangement of wing feathers? The overwhelming concensus is that it could scarcely fly at all, if by "flying" we mean maintaining itself in the air against gravity by flapping its wings. As de Beer (1954:52) pointed out, the short coracoid bone and the structure of the crista pectoralis of the humerus both suggest that the pectoral musculature of *Archaeopteryx* was much less developed than it is in modern flying birds. De Beer (1954, 1964) also placed great emphasis on the lack of a keel on the sternum as an additional indication of weak breast muscles. A careful reading of the 1954 monograph, however, shows that the structure of the sternum is known only tentatively (in spite of the neatness of the reconstruction in de Beer's Figure 4, redrawn as if definitively known by Swinton, 1960). The sternum as reconstructed by de Beer seems inadequate to support the pectoral musculature necessary even for gliding. A smaller structure in the Berlin specimen has been tentatively homologized with the bone de Beer believes to be the sternum of the British Museum specimen. The skeleton of the former is believed to have been less completely ossified than that of the London bird and thus probably represents a younger individual (de Beer, 1954:41). De Beer's drawing suggests to me the ossified base of a partly cartilaginous sternum, and, indeed, this possibility de Beer himself (1954:21) briefly mentions. That birds with largely cartilaginous sterna are capable of adequate flapping flight is well illustrated by the precociously flying chicks of modern gallinaceous birds. I regard the sternal structure of *Archaeopteryx,* therefore, as an open question and would not use it as evidence either for or against the ability to fly.

There are additional anatomical points, however, which favor the viewpoint that *Archaeopteryx* was a good glider but a poor flier. The structure of the elbow joint was too weak to withstand a powerful down stroke (Savile, 1957:222), and it is doubtful whether the bones were pneumatic as in modern birds. The long, rather rigid tail would not permit the maneuverability typical of bird flight as we know it, yet was admirably adapted to gliding. Additional evidence on this matter is presented by de Beer (1954, 1964) and Savile (1957).

In any case, we do know that there existed, in the late Jurassic, a creature that had developed a pennaceous feather like those of modern birds and was "appreciably advanced aerodynamically" (Savile, 1957:222), although not for a type of aerial locomotion like that of later birds. A new reconstruction of *Archaeopteryx* is presented on Plate I.

Theories on the Origin of Feathers

Leaving *Archaeopteryx* for the time being, we now turn to two controversies, which are often discussed separately without thinking through to the connective implications involved. The two questions are these: Which is the more "primitive" kind of feather in evolutionary sequence—the pennaceous (typical contour) feather or the plumulaceous (down) feather? And what was the original biological role of feathers—did they evolve as an aerodynamic device or did they develop as a mechanism assisting in the regulation of body temperature in connection with the evolution of homoiothermy (warm-bloodedness)? It is obvious that feathers perform both roles in living birds, but there are two distinct schools of thought as to which came first.

Much of the modern secondary, or synthetic, literature seems to favor the theory that feathers evolved from reptilian scales as a thermoregulatory device. Most such statements are brief, as for example: "The fossil, lizard-like bird *Archaeopteryx* . . . had feathers, *which shows* [italics added] that it was warm-blooded" (Heinroth and Heinroth, 1958:9); "It is likely that in evolutionary history the function of heat regulation came first. The two main functions of heat conservation and flight are indeed to-day performed by feathers of different types [i.e., down feathers and contour feathers, *but* see beyond]" (Young, 1962:432); "Feathers probably evolved from reptilian scales into a primitive, heat-conserving, fluffy insulation, and later into highly complex epidermal structures" (Welty, 1963:30); "It seems probable that feathers evolved to conserve heat and make homothermy possible, before they were used for flight" (*ibid.*:479); "It seems most likely that feathers originated as heat insulators and that they were later elaborated to facilitate gliding through the air" (Simkiss, 1963:44). See also Swinton (1960:11) and Lanyon (1964:5).

The most detailed statement I have found embodying this viewpoint of feather evolution is that of Van Tyne and Berger (1959:71), quoted here in full:

"It is probable that in their evolutionary history birds began with a covering of scales and a few feather filaments (cryptoptiles) scattered between them. As birds became homoiothermous ('warm-blooded') the filaments became of survival value as an insulating layer and in the course of evolution became more abundant and longer. The sequence of these ancestral stages, as now generally accepted, may be outlined thus:

"1. Cryptoptiles: Theoretical simple filaments which formed the covering of the primitive birds of earlier geological ages.

"2. Neossoptiles (nestling feathers).
    a. Protoptiles.
    b. Mesoptiles.

"3. Teleoptiles (adult feathers)."

Mayr (1959) was quite properly critical of this summary, stating "The phylogenetic sequence of feather types . . . is certainly not generally accepted. Personally, I find very persuasive the arguments of those who, like Portmann, demonstrate that all downy feathers are secondary derivations." But a year later, we find Mayr (1960:369) making this statement: "There is every reason to believe that the group of reptiles ancestral to the birds already had feathers, even though they had been acquired either for temperature control, as an epigamic character, or in some other way not connected with flight." Since Mayr had already rejected the theory that the primitive feather was a down, we are left with an ancestral reptile evolving *contour* feathers "in some . . . way not connected with flight." This theory seems highly dubious at best and certainly does not warrant the use of the phrase "there is every reason to believe. . . ." Justification could be attained by a semantic hedge if "some . . . way not connected with flight" were permitted to include jumping, parachuting, and gliding.

Let us return briefly to *Archaeopteryx,* recalling that it was clearly adapted to an arboreal habitat (de Beer, 1954:52), it was well on its way anatomically toward being a typical bird, it was probably an excellent glider but incapable of sustained flight, and, most important, it had already acquired typical pennaceous contour feathers. If the proponents of the theory that simple downs preceded pennaceous feathers are correct, we must push the origin of feathers well back before *Archaeopteryx* because, by the time *Archaeopteryx* appeared, the feathers, and indeed the whole aerodynamic system, had become quite complex and relatively well integrated. We are asked to envision a creature, which had evolved a downy covering as an adjunct to the beginnings of homoiothermy, and *then,* in some way, had modified these fluffy epidermal outgrowths into something that would in some way assist that creature in gliding among the branches of trees (modified *some* of them, that is, as a portion of the downs must have been retained as downs). I am indebted to my colleague Mary Dawson for the mental image of this hypothetical animal as something like a great leaping dandelion head gone to seed.

I believe, as do many others, that evolution in general and morphogenesis in particular have tended whenever possible to follow the simplest and most direct route. Examine any feather, contour or down. This is a rather complex organ with an elaborate ontogeny. Had the primary "need" of the avian ancestor been for an epidermal outgrowth, which would be useful as a thermoregulatory mechanism correlated with the attainment of warm-bloodedness, why "bother inventing" anything as complex as a feather? Hair would have been much simpler! Although there are several references in the literature to a "frayed scale" as the ancestor of an insulating down-feather, the latter organ is so complex—especially in its ontogeny—it is difficult to understand the adaptive advantages of the necessary intermediate evolutionary stages. And I should point out that several species of living reptiles have attained various levels of thermoregulation *without* any development of epidermal structures (see Hutchison *et al.,* 1966, and references quoted therein).

In connection with the use of feathers as a temperature regulator, I must make an important point: In spite of such statements as that of Romer (1962: 132), in most birds down feathers do *not* "underlie the contour feathers over much of the body of the adult, forming the main insulation." Although the proximal portions of many body contour feathers are quite plumulaceous, true adult body downs occur in relatively few orders of birds and are often sparse. The "main insulation" in most adult birds is *not* the down but the contour feathers, which are capable of erection and compression through a complex system of feather muscles (Stettenheim *et al.,* 1963), using entrapped air as an insulating layer. Many downy young birds have, in fact, relatively poor temperature control, at least at first. If, therefore, feathers originally evolved as a downy insulating layer and were later modified for an aerodynamic role, a completely new mode of the use of feathers to regulate temperature must have evolved *after* the development of the pennaceous feather. This *surely* is the long way around!

A Proposed Sequence of Feather Evolution

It is time, I think, to outline what I believe may well have been the sequence of events in the early evolution of birds. Several authors have shown rather conclusively that the early theories of the origin of bird flight, based on a hypothetical running animal that gradually took to the air by leaping and flapping its forelimbs, have no validity. The concensus is that *Archaeopteryx* and its immediate ancestors were arboreal, derived, no doubt, from terrestrial pseudosuchian reptiles. De Beer (1954) gives a thorough review of the evidence for the arboreal adaptation of *Archaeopteryx*.

I have seen nothing in the more recent literature that improves in any important way on the "proavian" theory of Heilmann (1927), as a projection of the evolution of birds backward from *Archaeopteryx*. True, some of our evolutionary concepts and much of our vocabulary have changed since the appearance of Heilmann's brilliant work. Today, for instance, we would not say that "by the friction of the air, the outer edges of the scales [became] frayed . . ." in describing the evolution of feathers from scales on the forelimb. But the general sequence of events postulated by Heilmann is, to me, by far the most logical explanation of the pre-*Archaeopteryx* evolution of birds from reptiles.

We begin with a highly active arboreal member of the pseudosuchian group of reptiles. Let us suppose that this animal had a row of somewhat elongated scales along the trailing edge of its forelimb. It is possible, as Heilmann states and shows in his restoration (*loc. cit.*:200), that these elongated scales developed along other edges of the body as well (see also the excellent plate of "proavis" by Burian, *in* Augusta, 1961:93). However, for simplicity we shall concentrate on the forelimb. As Savile (1962) showed, the slightest fringe of feather-equivalents would have an adaptive advantage in "parachuting" — the stage between simply falling and true gliding. It involves "balance but generally little or no steering. It is clearly adaptive in protecting from injury in accidental falls, as an escape mechanism, and in pursuit of prey" (Savile, 1962:161). There is no reason to doubt that such a selectively advantageous character would be retained and "improved" by the further elongation of the scales in question. As this lengthening took place, two things eventually became desirable: a stiffening mechanism and a way of lessening the weight of the long scales so that the forelimb would not be encumbered or thrown off balance during non-gliding use. Although we do not have direct evidence of the intermediate stages, the end-product of the evolutionary response to these "needs" must have resembled the present flight feather in having a stiff supporting central shaft and an elaborate lateral system of barbs and barbules, the whole combining strength with lightness.

Now, if these scale-feathers were really getting long enough to be useful adjuncts, first to parachuting and then to gliding, they were also becoming vulnerable. In leaping and landing among trees and branches, the reptile-bird might easily damage or break these projecting objects. It would be of great survival value if they could be replaced individually and periodically. In discussing the origin of feathers, some of my friends have suggested that I must explain the change in method of replacement of epidermal outgrowths, since reptiles "shed their skins" in one sheet or in large pieces and birds replace feathers at individual loci. Dr. Mary Dawson pointed out to me, however, that this is a straw man. The reptiles we know best are the snakes and lizards, which do indeed shed their epidermal covering in sheets. But the closest living reptilian relatives of birds are not the snakes and lizards; they are the crocodilians, which replace the outer layers of scales individually. It is not too far-fetched an evolutionary step to imagine the transition between such a surface replacement of a single scale and the invagination into a follicle system for growth of a new epidermal structure, as we know it in feathers today. The impression of the wings of the British Museum specimen of *Archaeopteryx* suggests that symmetrical replacement of individual remiges had already evolved, because the first (innermost) primary of each wing appears to have been growing.

Preadaptation in Feather Evolution

One of the most important points in my line of reasoning becomes evident when we examine a body feather of a bird. Note that it—and virtually every other feather except extremely specialized ones—is in essence a miniature of the large flight feather. It has the same stiffening shaft down the center and a strong but light-weight web on either side. In other words, the structure that we know to have been present in *Archaeopteryx,* and used in its gliding or primitive flight, is present in only slightly modified form all over the body of living birds. To me this strongly suggests that feathers represent an excellent example of *preadaptation.* This term, as discussed by Bock (1959) and Bock and von Wahlert (1965), has been applied principally to single structures which originally evolved in connection with a specific biological role but which were present, available, and suitable to perform quite a different role when the "need" arose. Any later modifications to such a structure or organ will be in response to selective pressures connected with *both* of the roles it now performs. The case of feathers is somewhat different, according to my theory, in that the flight feathers continue to perform their original role without any important structural modification (although variations in shape reflect the kinds of flight found in living birds; Savile, 1957). With the advent of warm-bloodedness and the need of an external heat regulator, however, the already existing genetic potential for the modification of scales into feathers could be extended to include the entire body *without* any major morphological change in the original feathers which were still performing their original aerodynamic role. The morphological changes that later resulted in the various kinds of body feathers (including the downs) in modern birds would be considered *postadaptive* and correlated with the many biological roles now performed by specialized feathers.

The general sequence of evolution from terrestrial reptile to actively flying bird, with reference to the occupation of successive "zones of adaptation," is excellently discussed and illustrated in a recent paper by Bock (1965). This paper emphasizes theoretical aspects of adaptation and scarcely mentions the actual morphological changes involved. In the one passage that does list such changes, Bock (1965:278) states: "The avian tibiotarsus and tarsometatarsus and the reversed pubis evolved in connection with bipedal locomotion; the reversal of the hallux with arboreal life; feathers, warm-bloodedness, and perfection of sight and hearing with a later stage in arboreal life; the wing and flight feathers, balance, and the beginnings of the rigid trunk with the stages of leaping, parachuting, and gliding." As should be obvious by now, I prefer to reverse the sequence of certain of these events. The critical point is the appearance of warm-bloodedness *vis-à-vis* the appearance of feathers. It is quite possible that *Archaeopteryx* was warm-blooded, but (*contra* Heinroth and Heinroth, 1958) this is not *proved* simply by its possession of body feathers. The latter may even have originally had an aerodynamic role, as they serve to smooth over irregularities in the body surface, such as the "pocket" at the junction of legs and body.

Thus it is quite possible that, by the time of the appearance of homoiothermy in birds, not only were the flight feathers present, but also the extension of the feathers onto the body may have been well under way. The *major* new addition to the feather system to permit it to assume an efficient thermoregulatory role would thus have been the musculature to control erection and depression of feathers. The period of the earth's history preceding and during the time *Archaeopteryx* lived is generally believed to have been characterized by tropical climatic conditions (Colbert, 1961:226, 230, 234 ff.) so the suggestion would be further buttressed that the perfection, if not the initial development, of an epidermal thermoregulatory mechanism (including the evolution of natal and other downs) may have taken place with a later climatic cooling.

Conclusion

As I warned at the beginning of this paper, a large portion of the foregoing is speculation, a search for what seems to me to be the most probable of a number of proposed sequences in the evolution of birds in general and of feathers in particular. This and similar papers will continue to be mere exercises in logic until we have further tangible evidence. The three specimens of *Archaeopteryx lithographica* have allowed us to determine a great number of facts about one specific stage in the evolution of birds from reptiles. Not inconceivably, later or earlier stages will some day be found. In fact, it is a little surprising that all of the known Jurassic bird fossils appear to be of a single species. In a recent *tour de force* of deductive reasoning, Brodkorb (1960:47) guessed that the Jurassic avifauna may have consisted of 100 contemporaneous species. Much of the conjecture about whether or not *Archaeopteryx* was on the "main line" of avian evolution would be cleared up if we should find a contemporary fossil of another species. Let us all, therefore, fervently hope that our colleagues, the paleontologists, keep on digging!

NOTE BY THE ILLUSTRATOR

Since the finding in 1861 in the Bavarian lithographic limestone of first a feather and then, later the same year, a complete skeleton of a feathered creature, the uproar has continued — at first strident and then gradually more muted. That the fossil is a bird seems to have been fairly well established over the intervening years. However, what kind of bird? How and why did it develop as it did? What was its color? What did it eat? Where did it live?

Although such questions did not seem to bother early writers, preparators, and artists, and — from available pictorial evidence — do not seem to disturb unduly quite a few of the contemporary, they have led to considerable study on the part of both the author and the illustrator of the present article.

Dr. Parkes has concerned himself with an attempt at dispersing some of the muddled thinking surrounding the "bird" itself and its possible ancestry. How and why did the reptilian scales covering the body change and develop into feathers? How was this change related to the ability of *Archaeopteryx* to fly, if we include gliding in "flying"? As the illustrator, I have attempted to solve some of the difficulties inherent in translating a skeleton into a pictorial representation.

When I painted my first representation for *Life* magazine in 1957, the "best" authorities believed that *Archaeopteryx* had six primaries; the illustration did not attempt to fudge and made the number clearly obvious in an attempt to stimulate some thinking and controversy which never came about because of the lack of subscriptions to *Life* from the scientific community. In the second representation, which I drew for the *Life* Nature Library volume "The Birds," the primary count had advanced to eight (because of the limitation to two colors, only the skeleton in its matrix was drawn in color while the reconstruction of the bird was in black and white, leading to various conclusions that white was the most primitive color). There has never been, in our opinion, an adequate full-color representation of *Archaeopteryx* in its natural habitat, in the act of catching and eating the prey which seems at this time the most logical.

In the earlier painting I showed *Archaeopteryx* feeding on a dragonfly (somewhat against my will, as I believed that the likelihood of *Archaeopteryx* snapping for dragonflies was rather dubious), because most of the leading "authorities" refused to hazard a guess as to what its food may have been.

At that time my feeling was that *Archaeopteryx* might well have been a carrion feeder (and I still believe that, under favorable circumstances, it may have been). Dr. Parkes, however, has convinced me that small reptiles were a more logical prey than insects, roaches possibly excepted.

I believe that the tan and brown colors shown here are more plausible than the bright colors shown by Heilmann, Knight, Burian, and others. I have tried to show all the controversial aspects of *Archaeopteryx* as clearly as possible (the number of primaries, the use of the claws on the wing, the method of grasping a branch, the method of feeding, and the method of flying/gliding) so that subsequent investigators and illustrators will have a target at which to shoot.

I believe, along with Dr. Parkes, that more digging is required, in search of the "missing links" or "proavis," and that further finds and further study will supply us with fascinating material for controversy. — Rudolf Freund, R.D. 2, Collegeville, Pennsylvania.

Summary

The Upper Jurassic species *Archaeopteryx lithographica,* although reptilian in many of its anatomical characters, had pennaceous contour feathers like those of living birds. While probably not capable of flapping flight, it appears to have been an excellent glider, well adapted aerodynamically for this type of locomotion. The author believes that feathers evolved originally from reptilian scales in a leaping arboreal "proavian," as postulated by Heilmann. He rejects the twin theories, that feathers evolved originally as a thermoregulatory device and that plumulaceous downs preceded pennaceous feathers, as illogical and requiring a roundabout series of evolutionary steps.

Acknowledgments

This paper is an outgrowth of a study on natal downs of birds, conducted jointly with Dr. George A. Clark, Jr. and supported by National Science Foundation Grant No. G-9039. I am indebted to Dr. Clark for the stimulating discussions of feather origins and allied subjects that provoked me into further reading on this topic. Other colleagues who have given me the benefit of some of their thoughts include Craig C. Black, Mary R. Dawson, Rudolf Freund, Mary A. Heimerdinger, Philip S. Humphrey, and Richard Lund. The photograph of the *Archaeopteryx* feather in the Institut für Paläontologie und Museum der Humboldt-Universität zu Berlin was supplied through the courtesy of Drs. Hermann Jaeger and Erwin Stresemann.

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THE ACTIVITIES AND COACTIONS OF ANIMALS AT SAPSUCKER TREES[1]

William L. Foster and James Tate, Jr.

Photographs by the authors

Feeding on tree sap is a common trait among woodpeckers. This is especially true of the Yellow-bellied and Williamson's Sapsuckers (*Sphyrapicus varius* and *S. thyroideus*), two species in which the habit is practically "a way of life." Also common, though not as widely known, is the habit among other species of birds, some insects, and even a few mammals of feeding repeatedly on the sap inadvertently supplied by the sapsuckers. The result is a complex situation wherein a species, through a specialized habit, attracts to its feeding area a host of animals which vie with one another, establishing a pronounced social order or hierarchy. We studied several feeding areas of the Yellow-bellied Sapsucker, paying particular attention to the activities and interrelationships of the visiting birds and other animals with a view to determining the factors accounting for their behavior.

Methods of Study

We made our observations at the University of Michigan Biological Station, Cheboygan County, near the northern tip of Lower Michigan (see Figure 1): intermittently at two sapsucker feeding areas, Area A in 1963 and Area B in 1964, and more intensively at five areas, Areas C1, C2, C3, C4, and C5 in 1965. Altogether we spent 250 hours, recording minute-by-minute activities at the seven feeding areas, and an equal amount of time in the field, watching the sapsuckers themselves and investigating the activities at their nests. From 12 June to 7 August 1965, we conducted a concentrated, day and night study of four areas (C1-4) to obtain quantitative data on activities and coactions. During night observations we made intermittent use of either flashlights or infra-red light from a U. S. Navy surplus snooperscope and sniperscope. For identification purposes we captured bats with mist nets, and insects with insect nets and flypaper placed near the sapsuckers' feeding holes. We have deposited representative specimens of the insects and bats in the scientific collections at the University of Michigan Biological Station where they are available for reference.

At two of the areas we used blinds, one at a height of 40 feet in an adjacent maple (C1) and another on a 24-foot tower (A), 10 and 15 feet respectively from the drillings. All of the other areas we observed from vantage points on the ground.

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[1] Contribution from the University of Michigan Biological Station

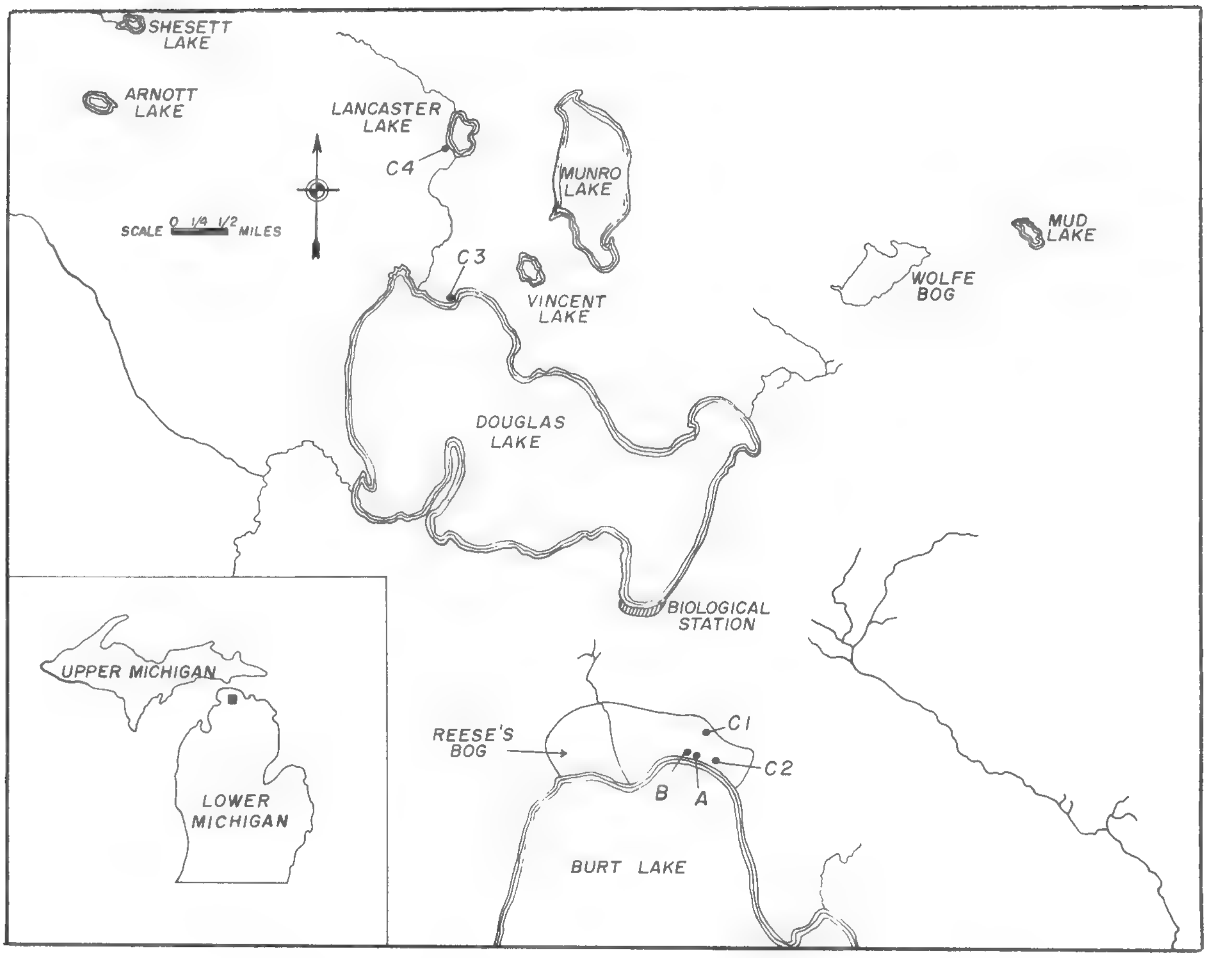

SHESETT LAKE
ARNOTT LAKE
LANCASTER LAKE
C4
SCALE 0 1/4 1/2 MILES
MUNRO LAKE
MUD LAKE
C3
VINCENT LAKE
WOLFE BOG
DOUGLAS LAKE
BIOLOGICAL STATION
UPPER MICHIGAN
LOWER MICHIGAN
REESE'S BOG
C1
C2
B
A
BURT LAKE

Figure 1. Map showing the vicinity of the University of Michigan Biological Station in northern Lower Michigan and the location of six feeding areas of the Yellow-bellied Sapsucker.

The Environment

The forested acreage occupied by sapsuckers in the vicinity of the Biological Station is comprised primarily of second-growth timber replacing the virgin stands that were lumbered and burned prior to 1900. For nesting habitat the sapsuckers select cool areas at low elevation, often adjacent to bogs or lakes, where there is at least a scattering of deciduous trees, if not an extensive stand. The trees from which the birds obtain their sap during the breeding season vary greatly in distance from the trees in which they nest.

Four of the areas under our observation (A, B, C1, and C2) were on the north shore of Burt Lake in Reese's Bog, an ancient lakeshore bog grown up extensively to balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and arbor vitae (*Thuja occidentalis*). Intermingled with the conifers were occasional clumps of paper birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*).

We located the nest of each of the pairs that fed in Areas A, B, and C1. All the nests were in holes in live trembling aspens, from 40 to 60 feet above the ground. We discovered Area C2 after the fledging of the young.

Area C3 was 75 yards from the shore of Lancaster Lake in an upland forest of large-toothed aspen (*P. grandidentata*), maple (*Acer* spp.), and paper birch. The nest of this pair, in a large-toothed aspen, we found after the young had fledged. Area C4 was on the northwest shore of Douglas Lake in the front yard of a private cottage. We failed to locate the nest of this pair.

The Sap Flow in Trees

Sapsuckers typically use woody dicotyledonous plants and large woody gymnosperms. In these plants the woody core of the tree, composed largely of xylem vessels and tracheids, is of little use in transporting liquids. The outermost cells of the xylem carry most of the water and mineral nutrients from the roots to all parts of the tree. The phloem, a layer which lies outside the xylem, transports the products of photosynthesis from the leaves to all parts of the tree. It is into the phloem that the sapsucker digs its typical squarish holes (Figure 2).

Although knowledge of the sequence of sap flow in the phloem throughout the year is still incomplete, certain features, that are well understood, are of interest here. During the winter months in northern latitudes, roots and stems of dormant trees store nutrient materials in relatively inactive forms. Sap in the phloem is reduced in sugar content and there is little flow from one area to another. On warm days there may be some flow, especially on the sunlit side of branches, and at such times sap might flow from old sapsucker holes in these areas (see Kilham, 1958a:111).

With the spring warmth the sap is reconstituted from stored nutrients, and the water flow in the xylem increases. At this time humans harvest maple sap and sapsuckers return north. During this period of "upward" flow of sap, the sapsuckers often make holes in single rows around the trunk (Figure 3A), drilling most commonly in those trees which flower and leaf out first in the spring. The birches, which will become the major feeding trees in the summer, leaf out later.

During the summer, sap flow is complex, with different nutrients simultaneously passing in two directions within a single phloem tube. The major trend of flow, however, is "downward" from the area of production — the leaves or the photosynthetic portions — toward the areas of consumption and growth. The volume and quality of flow on any given day are related to the rate of transpiration and photosynthesis in the tree which is in turn affected by the weather. On humid, still, cloudy days sap flows the least; while on dry, breezy, clear days the flow is the greatest. The varying rate of flow affects the amount and type of activity engaged in by the sapsuckers and other visitors to the trees.

How Sapsuckers Feed on Sap

The sapsucker feeds primarily on insects and obtains most of them from the crowns and boles of trees near the feeding area and from around the holes it drills for sap. Judging from food remains in the sapsucker nests and from observations of captures, mayflies and ants are by far the most important insects in the sapsucker's diet. The bird usually captures mayflies by flying against the outer branches of trees and flushing the insects from the leaves where they rest in large numbers through June and early July. It captures ants most commonly from the feeding tree, but also takes them from the trunks and branches of nearby trees, and, sometimes, even from the ground (Bailey, 1928). Later in the season it more frequently takes flies and vespid wasps, nearly always near the feeding holes. Although the sapsucker often jabs with its bill at insects flying near the holes, it seldom catches them.

Typically a sapsucker, on obtaining a mouthful of insects, flies to the feeding tree, where it works the insects into the wet sap and forms a bolus which it either consumes or takes to the young. When taking large insects, it deals with them in a special manner, carrying them to a favorite knot or sap

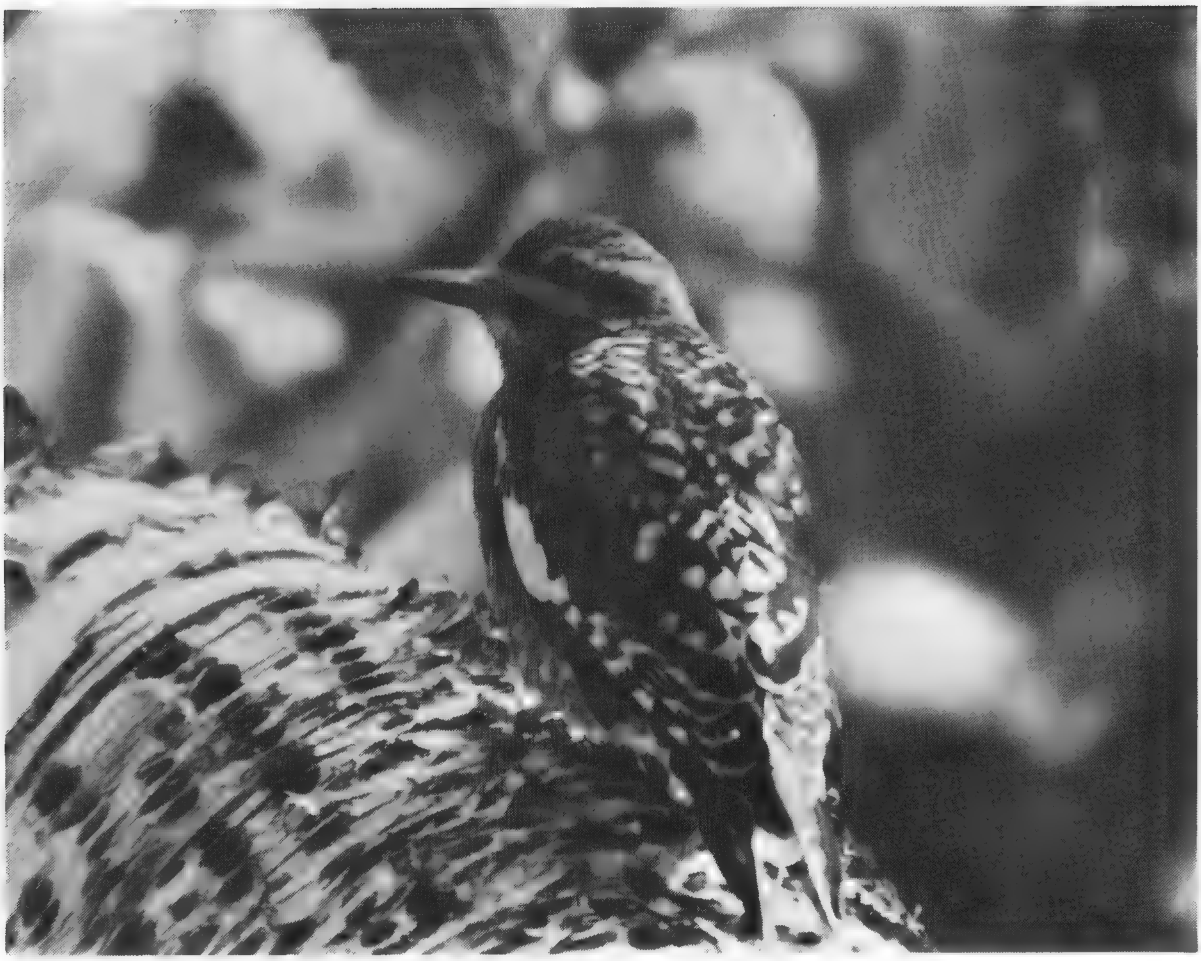


Figure 2. Juvenile Yellow-bellied Sapsucker at summer feeding holes in a paper birch.

hole and beating them to a mush. It then dips and works the softened insects in the sap for several minutes before eating them, or taking them to the young. When the sap is concentrated, sapsuckers will take it separately, tilting the head back and drinking the liquid as if it were water, or with their brush-like tongue licking the sap from the holes and from the surface of the bark.

Although the Yellow-bellied Sapsucker feeds in the winter and during migration on the sap of a wide variety of trees and shrubs including evergreen trees (see McAtee, 1911), it generally prefers paper birches during the midsummer period at the Biological Station. A regular seasonal pattern of feeding habits in northern Michigan is as follows.

The sapsuckers arrive during the second and third weeks in April (Wood, 1951:258) before the birches are fully leafed out. At this time they select various trees and shrubs, including red pine (*Pinus resinosus*), trembling aspen, and maples from which to obtain stored phloem sap and frequently drill single, horizontal rows of holes spaced evenly about the trunk (Figure 3A). During the spring in New Hampshire, Kilham (1964:522) found that the birds frequently choose hemlocks and aspens but in Michigan they most often select maples and elms (*Ulmus americana*) for early feeding. Not until late May and early June do they begin working extensively on the trees, usually birches, in what will become the main feeding area for the summer. Quite often this area will contain trees that have been drilled slightly the preceding summer. The sapsucker makes new holes above the old ones, effectively obtaining phloem sap that is moving downward in the tree. The activity of the sapsucker and some of the other tree visitors tends to enlarge some of the holes, which often remain active for long periods of time.

Sap Feeding During the Nesting Season

The nest of the sapsucker is often some distance from the feeding tree: the nests in Areas A and B were 200 yards from the respective feeding areas; the nest in Area C1 was 75 yards from the feeding area. By using two-way radios, one of us at the feeding tree could communicate with the other at the nest and thus inform each other of the departure of an adult from the feeding tree, and *vice versa.* In this way we were able to follow the feeding-nesting routines of most pairs.

Either parent could make the direct flight from feeding tree to nest at Areas A and B in 25 seconds (24 feet per second) and at Area C1 in eight seconds (28 feet per second), although we found that the movement of sapsuckers between nest and feeding area was not always direct. As a rule, the parents flew straight to the nest when they had gathered sap and insects at the feeding tree and were intent on feeding the young. Arriving at the nest area, they often went immediately to the nest-hole. Early in the nestling period, they entered the cavity to feed the young and emerged carrying out fecal sacs and woodchips. Later, nearer the fledging date, they stayed outside the cavity, while the young appeared at the nest-hole and reached for the food.

Many times after feeding the young the parents lingered in the area, where they cleaned their bills or began to hunt insects on the way back to the feeding tree. During the time of the high population of mayflies near the lake shore, the parents developed a common pattern of activity. Each one came to the feeding area from the nest, fed on sap, flew toward the lake, appeared a few minutes later at the feeding area with insects protruding from its mouth, worked the insects in the sap, and flew with the bolus directly to the nest.

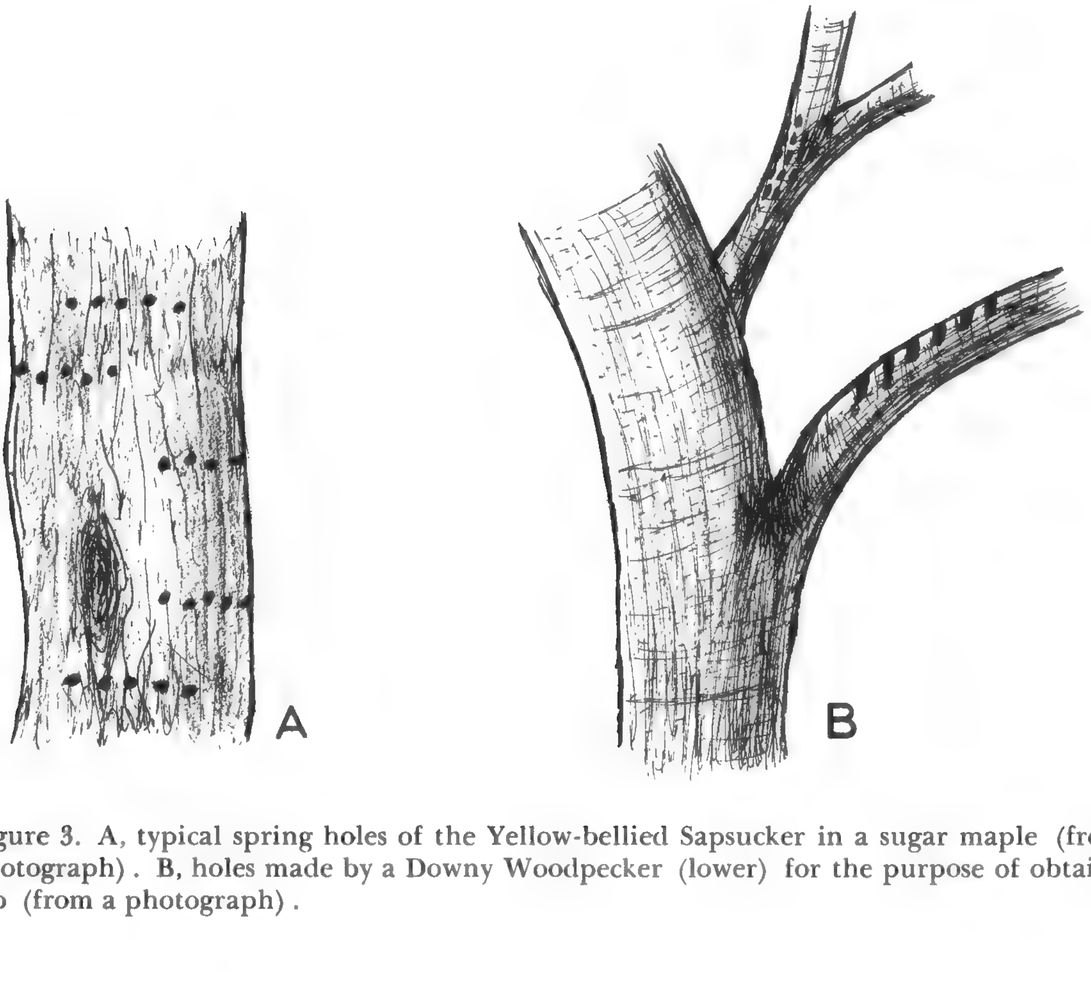


Figure 3. A, typical spring holes of the Yellow-bellied Sapsucker in a sugar maple (from a photograph). B, holes made by a Downy Woodpecker (lower) for the purpose of obtaining sap (from a photograph).

Bringing the Young to the Feeding Tree

In two nests (A, C1) that we observed during the fledging days, the parents drew the young from the nest-hole by holding the food away. Near the end of the nestling period we saw one young sapsucker come more than half-way out of the hole to reach for food, and then retreat, but we never saw the young return to the hole after they fledged. The fledging of the three to six nestlings in a single brood may be spread over two or three days. At Area B, one young was at the feeding tree while another was still in the nest-hole. During this time the parents were especially busy in feeding both the young that had fledged and those that remained in the nest-hole. In each case the young followed the parents to the feeding area in less than one day after fledging.

During the early days at the feeding tree, the young begged continually and did not feed themselves. As the post-fledging period progressed, the adults increasingly avoided the young. Within four or five days after fledging, the adult female no longer took part in their care. At every area we studied, the female either dominated one of the several trees in the area or went to a nearby area that the pair had used only occasionally before. In her selected area she tolerated neither the male nor the young. This segregation in separate feeding areas, with the male and young at the major feeding trees and the female alone, reduced the intraspecific competition for food.

Sap Feeding by Other Woodpeckers

The woodpeckers of the genus *Sphyrapicus* do not have a monopoly on the sap-feeding habit. According to Turcek (1954), four woodpeckers in Europe drill holes for the purpose of obtaining sap. He mentions the Great Spotted Woodpecker (*Dendrocopos major*) as showing this trait most frequently and gives scattered instances of it in the Black Woodpecker (*Dryocopus martius*), the Green Woodpecker (*Picus viridis*), and the Northern Three-toed Woodpecker (*Picoides tridactylus*). The Northern Three-toed Woodpecker also occurs in North America, but we know little about its habits, particularly its sap-drilling abilities.

A debate as to the prevalence of this habit in the Downy Woodpecker went on for several years until Forbush (1921) produced a convincing description and photographic evidence that it too drills sapsucker-like holes to obtain sap. We observed one male Downy Woodpecker, a regular visitor at a sapsucker tree, drilling for sap at Area C3. He cut a new distal hole on a branch that already had five holes along its length (Figure 3B) and then moved back toward the trunk to obtain sap flowing from the next hole. All the holes were proportionally wider and larger than those made by the sapsucker in the branch above. The incident occurred on a day when sap flow from the sapsucker holes was especially poor.

In none of these woodpecker species is the sap-obtaining habit as extensive as in the sapsuckers. The European species use sap only in the spring (Turcek, 1954) and their drilling seems to be very similar to the spring drillings of the Yellow-bellied Sapsucker. Furthermore, none of the European species has been reported taking sap to their young as do the sapsuckers.

Turcek (*loc. cit.*) reported visitors to the spring feeding tree of the Great Spotted Woodpecker to include individuals and mixed flocks of Great Tits (*Parus major*), Blue Tits (*P. caeruleus*), Marsh Tits (*P. palustris*), and Long-tailed Tits (*Aegithalos caudatus*).

Animal Associates

We identified arthropods, mostly insects, of nine orders and 22 families at the sapsucker trees. They were either feeding on the sap or preying on other insects. There were others unidentified. We found 20 species of birds significantly associated with either the insects or the sap and observed five species of mammals associated with sapsucker feeding trees (see Tables 1-3).

Insects at the Trees

Undoubtedly dozens of species of insects are associated with sapsucker drillings. We have found about thirty groups (species and families) of special importance because of their occurrence in large numbers or their consistent association with the sapsuckers (see Table 1).

Butterflies seldom land at the sap if other animals are at the holes. Even the presence of large numbers of vespid wasps cause the butterflies to move frequently and to constantly flick their wings while feeding. Two species, the mourning cloak and the tortoise shell, were the most common, although we frequently saw the other Nymphalidae mentioned in Table 1.

Moths—mostly members of the family Noctuidae—replace butterflies at the tree at night. Those in the genus *Catocola,* the underwings, were the most common except for the night of 5 August 1965 when we saw as many as fifteen of the large sphinx moths (Sphingidae) at Area C4. Northern flying squirrels preyed on the large moths when they could catch them.

Some of the insects and two groups of arachnids (Phalangida and Araneida) preyed on small insects that came to the sap. A single species of click beetle occurred at several feeding trees, but never in any numbers.

Fruit flies and other small dipterans often formed clouds around the holes. When these animals drowned in the sap, they formed part of the diet of the vertebrate animals feeding at the holes.

During most of the daylight hours, flies and hornets made up the bulk of the larger insects at the trees, and there were periods, in the morning and evening and on poor sap days, when flies were almost the only organisms recorded at the holes. The flies were subordinate to the hornets and fed only at a hole temporarily left vacant when two or more hornets, apparently battling over feeding rights, departed.

Birds at the Trees

Of at least 35 species of birds, reported to have been associated with sapsucker trees, 21 occurred in our study areas in summer and 20 were recorded at the trees (see Table 2). In addition, we recorded 13 species at our trees for which we could find no record in the literature. A few species consistently visited the sapsucker trees, some for insects, some for sap, and a few for both. We saw other species at every area, but none commonly and a few only once.

Hummingbirds. Four species of North American hummingbirds have been reported at sapsucker feeding areas (see Table 2). Of these, the Ruby-throated Hummingbird has been recorded most frequently. The Ruby-throated is the only hummingbird that occurs in northern Michigan and we have more records of visits in our study areas by this species than of any other bird, including the sapsuckers themselves.

Although Ruby-throated Hummingbirds came primarily to feed on sap (Figure 4), they also took insects. We saw the hummingbird catch insects, fly

TABLE 1

Arthropods Associated with Yellow-bellied Sapsuckers and Their Feeding Trees

Groups or species	*Feeding on insects*	*Feeding on sap*	*Serving as sapsucker food*	*Authority*
INSECTA				
Ephemeroptera				
Mayflies (mostly Ephemeridae)			X	Pers. observ.
Hemiptera				
Assassin bugs (Reduviidae)	X			Pers. observ.
Lygaeid bug (Lygaeidae) *(Ischnorrhynchus resedae)*			X	Pers. observ.
Homoptera				
Cicada (Cicadidae) *(Tibican canicularis)*			X	Pers. observ.
Coleoptera				
Lampyrid beetle (Lampyridae) *(Lucidota fenestralis)*	X			Pers. observ.
Click beetle (Elateridae) *(Aariotes fucosus)*		X		Pers. observ.
Ladybird beetles (Coccinellidae)			X	Pers. observ.
Lepidoptera				
Nymphalidae				
Red admiral *(Vanessa atalanta)*		X	X	Nickell, 1956; pers. observ.
Painted lady *(Vanessa cardui)*		X	X	Nickell, 1956; pers. observ.
Mourning cloak *(Nymphalis antiopa)*		X	X	Eifert, 1941; pers. observ.
Tortoise shell *(Nymphalis j-album)*		X	X	Pers. observ.
White admiral *(Basilarchia arthemis)*		X	X	Hansen, 1957.
Sphinx moths (Sphingidae)				
Hornworm moths *(Protoparce* sp.)		X		Pers. observ.
Big poplar sphinx *(Pachysphinx modesta)*		X		Pers. observ.
Noctuid moths (Noctuidae)				
Underwing moths *(Catocala relicta, C. ilia, C. cerogama, C. concumbens)*		X		Pers. observ.
Other small noctuids (including Geometridae and Tortricidae)		X		Pers. observ.

TABLE 1 (Con't)

Groups or species	*Feeding on insects*	*Feeding on sap*	*Serving as sapsucker food*	*Authority*
Diptera				
Wood gnats (Anisopodidae) (*Anisopus* sp.)		X	X	Pers. observ.
Fruit flies (Drosophilidae)		X	X	Pers. observ.
Common flies (Muscidae)		X	X	Pers. observ.
Blow flies (Calliphoridae) (*Lucilia illustris*)		X	X	Pers. observ.
Flesh flies (Sarcophagidae) (*Sarcophaga aldrichi,* and *S. coloradensis*)		X	X	Pers. observ.
Hymenoptera				
Sawflies (Tenthredinidae)			X	Pers. observ.
Ants (Formicidae) (*Camponotus herculeanus*)		X	X	Pers. observ.
Wasps (Vespidae)				
Bald-faced hornet (*Dolicovespula maculata*)		X	X	Kilham, 1964; Nickell, 1956.
Yellowjacket (*Vespula maculata*)		X	X	Pers. observ.
Small *Vespula* sp.		X	X	Pers. observ.
PHALANGIDA				
Daddy-longlegs	X			Pers. observ.
ARANEIDA				
Spiders	X			Pers. observ.

TABLE 2

Birds Associated with Feeding Trees of the Yellow-bellied Sapsucker

Species	*Feeding on insects*	*Feeding on sap*	*Seasons observed*[1]	*Authority*
Trochilidae				
Ruby-throated Hummingbird (*Archilochus colubris*)	X	X	S	Bolles, 1891; Freer, 1935; Kilham, 1953b; Nickell, 1956, 1965; Mitchell, 1919; Palmer, 1949; Saunders, 1936; Snyder, 1951; pers. observ. and others.
Anna's Hummingbird (*Calypte anna*)		X	S	Grinnell and Storer, 1924; Taylor, 1920; Wright and Wright, 1918.

TABLE 2 (Con't)

Species	*Feeding on insects*	*Feeding on sap*	*Seasons observed*[1]	*Authority*
Broad-tailed Hummingbird (*Selasphorus platycercus*)		X		Hall, 1938.
Rufous Hummingbird (*Selasphorus rufus*)		X	S	Jewett, *et al.*, 1953.
Picidae				
Red-bellied Woodpecker (*Centurus carolinus*)		X	W	McGuire, 1932.
Red-headed Woodpecker (*Melanerpes erythrocephalus*)		X	F,W,Sp	Kilham, 1958a.
Hairy Woodpecker (*Dendrocopos villosus*)		X	S	Kilham, 1965; Nickell, 1956; pers. observ.
Downy Woodpecker (*Dendrocopos pubescens*)	X	X	S	Bolles, 1891; Kilham, 1964; Nickell, 1956, 1965; pers. observ.
Northern Three-toed Woodpecker (*Picoides tridactylus*)		X	S	Bent, 1939.
Tyrannidae				
Great Crested Flycatcher (*Myiarchus crinitus*)	X		S	Pers. observ.
Eastern Phoebe (*Sayornis phoebe*)	X		S	Pers. observ.
Least Flycatcher (*Empidonax minimus*)	X		S	Pers. observ.
Sittidae				
White-breasted Nuthatch (*Sitta carolinensis*)	X	X	S	Pers. observ.
Red-breasted Nuthatch (*Sitta canadensis*)	X	X	S	Pers. observ.
Turdidae				
Robin (*Turdus migratorius*)	X		S	Pers. observ.
Sylviidae				
Ruby-crowned Kinglet (*Regulus calendula*)		X	W,Sp	Danforth, 1938; Taylor, 1920.
Vireonidae				
Warbling Vireo (*Vireo gilvus*)	X		S	Pers. observ.
Parulidae				
Black-and-white Warbler (*Mniotilta varia*)	X		S	Bolles, 1891; pers. observ.

Species	*Feeding on insects*	*Feeding on sap*	*Seasons observed*[1]	*Authority*
Parula Warbler *(Parula americana)*	X		S	Pers. observ.
Yellow Warbler *(Dendroica petechia)*	X		S	Pers. observ.
Cape May Warbler *(Dendroica tigrina)*	X	X	S, F	Kilham, 1953b; Marvel, 1948.
Black-throated Blue Warbler *(Dendroica caerulescens)*	X	X	S, F	Kilham, 1953b; Mousley, 1917; pers. observ.
Myrtle Warbler *(Dendroica coronata)*	X	X	Sp, S, F	Kilham, 1953a; Mousley, 1917; Stone, 1937; pers. observ.
Audubon's Warbler *(Dendroica auduboni)*		X	W, Sp	Danforth, 1938; Taylor, 1920.
Black-throated Green Warbler *(Dendroica virens)*		X	S	Nickell, 1965.
Blackburnian Warbler *(Dendroica fusca)*	X		S	Pers. observ.
Pine Warbler *(Dendroica pinus)*	X	X	S	Pers. observ.
Northern Waterthrush *(Seiurus noveboracensis)*	X	X	S	Pers. observ.
American Redstart *(Setophaga ruticilla)*	X		S	Pers. observ.
Painted Redstart *(Setophaga picta)*		X	W	Goodman, 1954.
Icteridae				
Baltimore Oriole *(Icterus galbula)*	X	X	W, S	Sykes, 1960; pers. observ.
Fringillidae				
Pine Siskin *(Spinus pinus)*		X	W	Batts, 1953.
American Goldfinch *(Spinus tristis)*		X	W	Batts, 1953.
Oregon Junco *(Junco oreganus)*		X	W	Taylor, 1920.
White-crowned Sparrow *(Zonotrichia leucophrys)*		X	W, Sp	Danforth, 1938.

[1] Seasons: S, summer; F, fall; W, winter; Sp, spring.

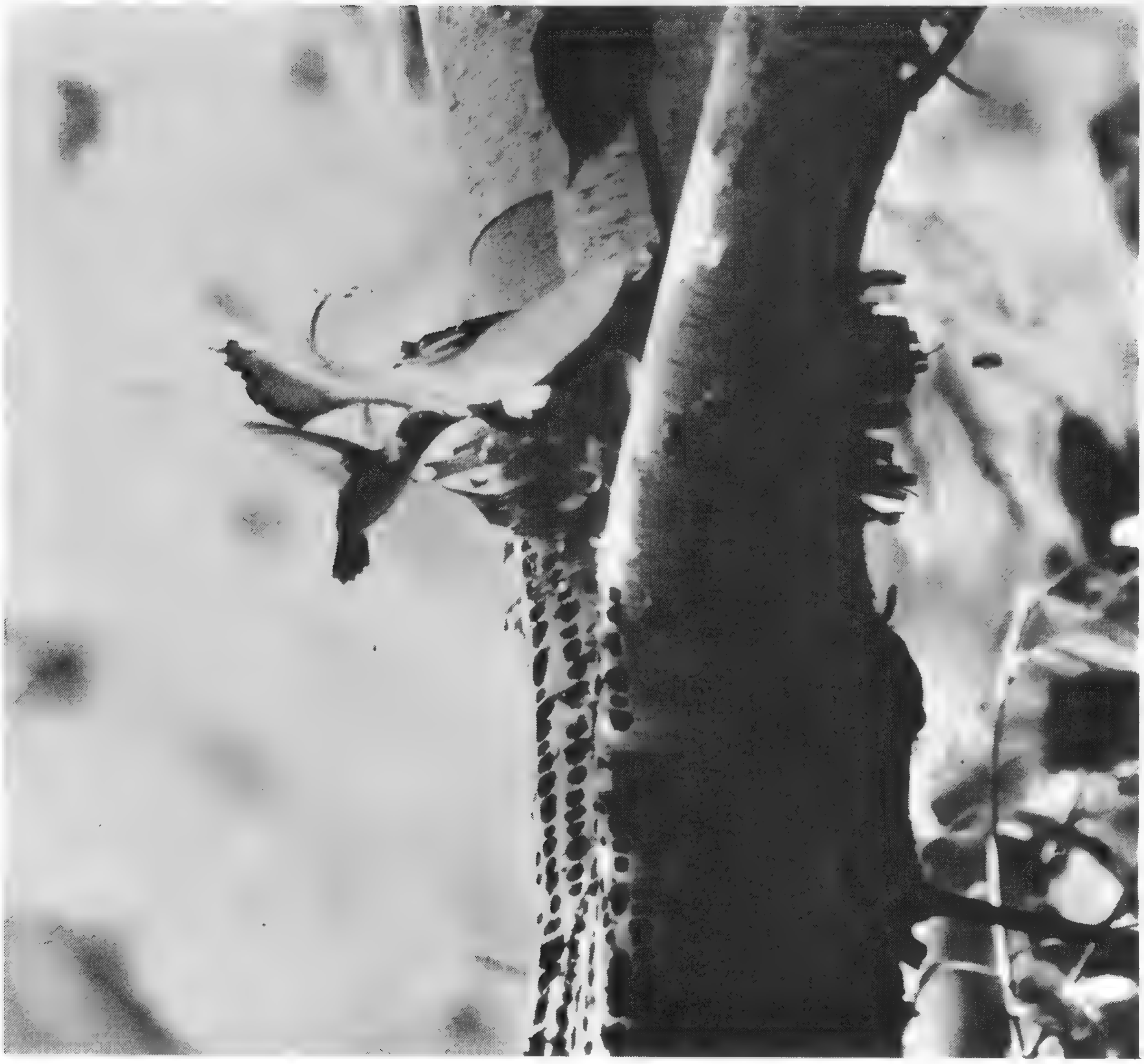


Figure 4. Ruby-throated Hummingbird feeding at sapsucker drillings.

back to a favorite perch, sit awhile, perhaps preen, fly out again, and catch more insects. This action, which took place in the immediate vicinity of the perch, sometimes continued for five minutes. All during the summer, the male hummingbird, being completely free of nesting cares, seemed to use the vicinity of sapsucker feeding trees as its activity area and, later in the season (August), the female too spent much of her time sitting near the sapsucker trees.

Never did we see two or more hummingbirds feeding peacefully together. Their actions toward one another throughout the period of our study were consistently belligerent and intolerant. We repeatedly noted the pendulum action described by Pitelka (1942:201) as "essentially an intimidation device." Squeaking, chattering, and chasing were common and increased during the summer, probably because the young and adults converged on the area after nesting. For example, during August, we recorded in Area A at least 30 encounters with almost continuous squeaking and chatter in one hour. A few times there was actual physical contact during these encounters.

Our observations at the feeding area revealed a segregation of hummingbird sexes — i.e., a tendency for the male and female Ruby-throated Hummingbird to feed in different places. Greenewalt (1960) also recognized this segregation at feeding areas. From 12 June to 7 August 1965, we kept quantitative data on hummingbird activity. Figure 5 shows the ratio of male-to-female visits, based on our 102 daylight hours of systematic observation at four sapsucker feeding areas. Area C1 is the only one with predominantly male visitors. The highest number of visits of hummingbirds of both sexes to one area in one hour was 82. This was in the early afternoon at Area C2. The lowest number of visits per daylight hour was zero at three areas.

The dominant sex visited the tree regularly throughout the day. The other sex usually appeared irregularly. Exactly how many individuals were involved is not known, but we saw five individuals at one time in Area C3. Mitchell (1919:42) collected six hummingbirds at a feeding tree and others still came.

During our observations at Area C4, we found a Ruby-throated Hummingbird nest 20 feet above ground and 10 feet out on the horizontal limb of a maple which was 50 feet from two paper birches used as sapsucker feeding trees. The proximity of this nest to the feeding area permitted us to view it as we made observations on the sapsucker feeding area. During incubation the female hummingbird left the nest at intervals and went directly to the holes to feed. Many times we saw her return to the nest at once or sit in the immediate area. Only a few times did her whereabouts elude us. After the young hatched, she fed them on sap and insects gathered at the tree. On 8 August, we color-marked the two young in the nest and several days later saw one of these young in the vicinity of the feeding area, flying slowly and deliberately from branch to branch. Saunders (1936:153) reported a hummingbird nest near a maple tree drilled with holes by sapsuckers.

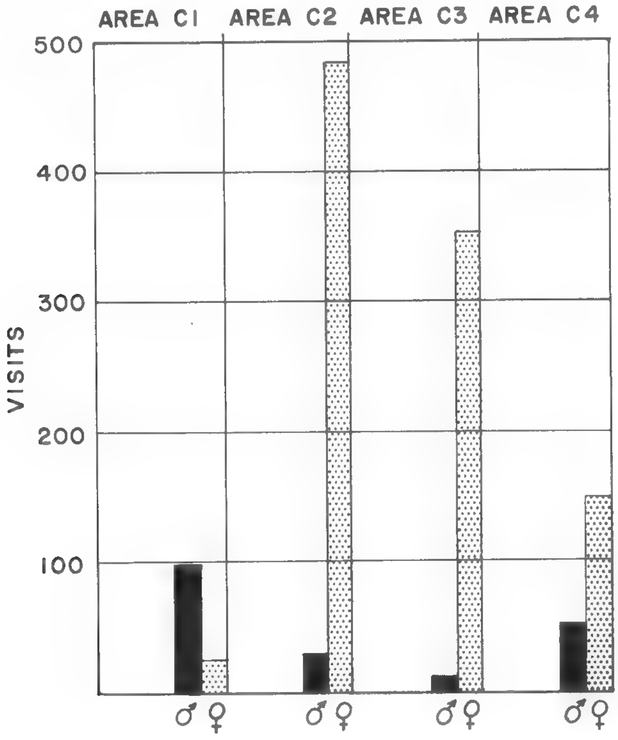


Figure 5. The number of visits made by male and female Ruby-throated Hummingbirds to four sapsucker feeding areas during June and July 1965. There was almost complete segregation of the sexes to different areas throughout the summer.

Five times we saw hummingbirds following (within inches) sapsuckers in full flight away from the feeding area. This happened one other time near the sapsucker nest. But following sapsuckers is rare, however, considering our 250 hours of observation. Red attracts hummingbirds, so it may be possible that the bright red on the head of the adult sapsucker acts as a stimulus, or it may be that the hummingbird has the habit of following sapsuckers to find new feeding areas.

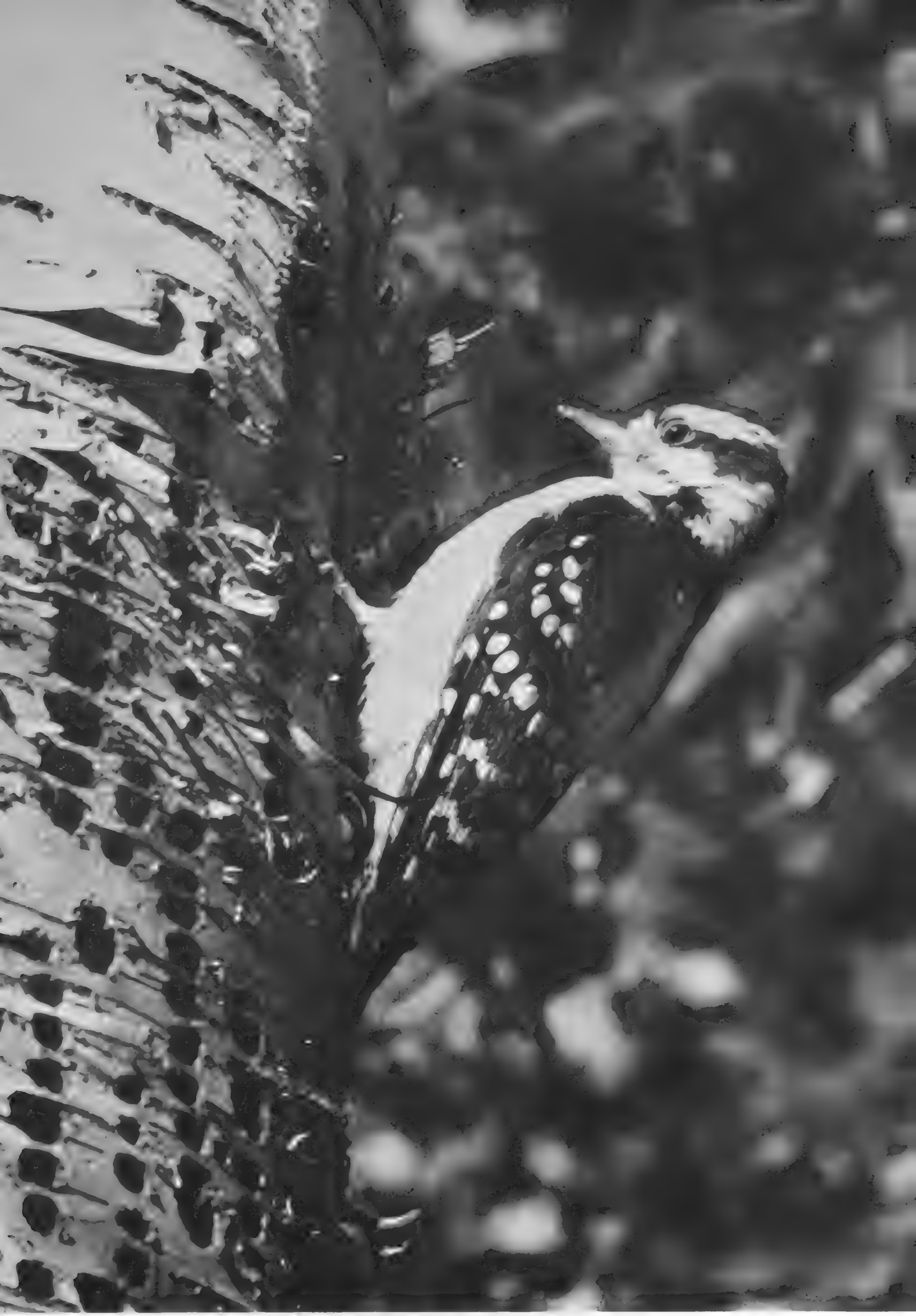


Figure 6. One of several Downy Woodpeckers at sapsucker feeding holes.

Woodpeckers. Five species of woodpeckers have been reported feeding at the drillings of sapsuckers (see Table 2). During our study, only two of these woodpeckers other than sapsuckers were associated with the drillings. We saw Hairy Woodpeckers only twice (Area C1), once taking sap. O. S. Pettingill, Jr. has motion pictures of a Hairy Woodpecker feeding during July on sap from drillings in a paper birch near our Reese's Bog areas. Kilham (1965:141-142) noted two instances of Hairy Woodpeckers feeding on sap at sapsucker holes, and another instance in which a Hairy Woodpecker, feeding near a sapsucker area, took no interest in the flowing sap, in contrast to a Downy Woodpecker which was a frequent visitor. Nickell (1956) found both a male and female Hairy Woodpecker feeding on sap at a paper birch in June.

Male and female Downy Woodpeckers were common visitors at three areas (A, C2, and C3), where we often saw several individuals (Figure 6). At least three females, one male, and one immature male visited Area C3. Intraspecific conflict was very evident, with the males dominating the females. Frequently, when a Downy Woodpecker was displaced from the holes, it moved to another branch and fed on insects or just sat still until given an opportunity to return. The Downy Woodpeckers consequently spent nearly as much continuous time at the feeding trees as the sapsuckers.

Flycatchers. Three species, the Great Crested Flycatcher, the Eastern Phoebe, and the Least Flycatcher, visited the sapsucker trees infrequently. We saw the Great Crested Flycatcher in Area C1 on five occasions, catching insects attracted to the sap.

We repeatedly saw phoebes near Area C3; a pair had a nest on a building close by and were at the tree feeding on insects once or twice for every twelve hours of observations. We recorded the Least Flycatcher in Area C1 where it fed on insects at the holes.

Nuthatches. We observed the White-breasted Nuthatch feeding on the sap and insects in Areas C3 and C4 (Figure 7). The Red-breasted Nuthatch visited four areas (A, B, C1 and C2). We never found both species in the same area, but they were present regularly in their respective areas. Evidently the habitat surrounding the feeding tree determined which of the nuthatches would be present. They ranked low in the interspecific social hierarchy but, like the Downy Woodpecker, when another animal displaced them from the holes, they merely fed on another part of the tree and returned to the holes at first opportunity. The nuthatches fed on the sap by dipping the bill and lifting the head as if drinking.

Warblers. We observed nine species of warblers associated with sapsucker drillings. Four other species, three of which do not occur commonly in Lower Michigan, have been reported by other observers (see Table 2). Warblers were irregular visitors at the holes. Their numbers increased as the summer progressed — probably due to the dispersal of young and adults after the nesting period. We observed all nine warblers taking insects and four—Black-throated Blue Warbler, Myrtle Warbler, Pine Warbler, and Northern Waterthrush—drinking sap. They placed their beaks in the hole and then raised their heads. Goodman (1954) found a Painted Redstart feeding at sapsucker holes. This bird, the fifth record for the species in southern California, remained in the area for several days.

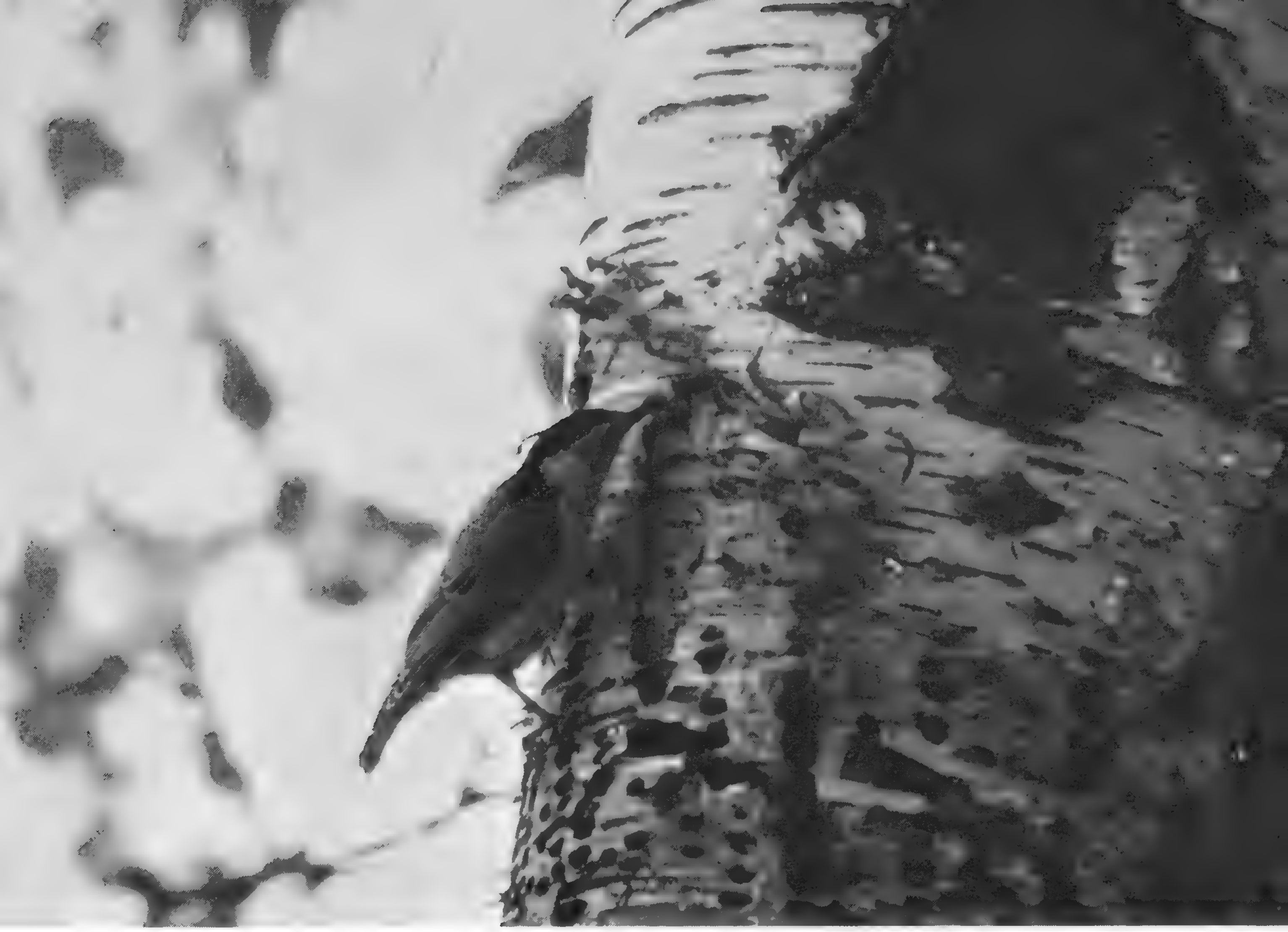
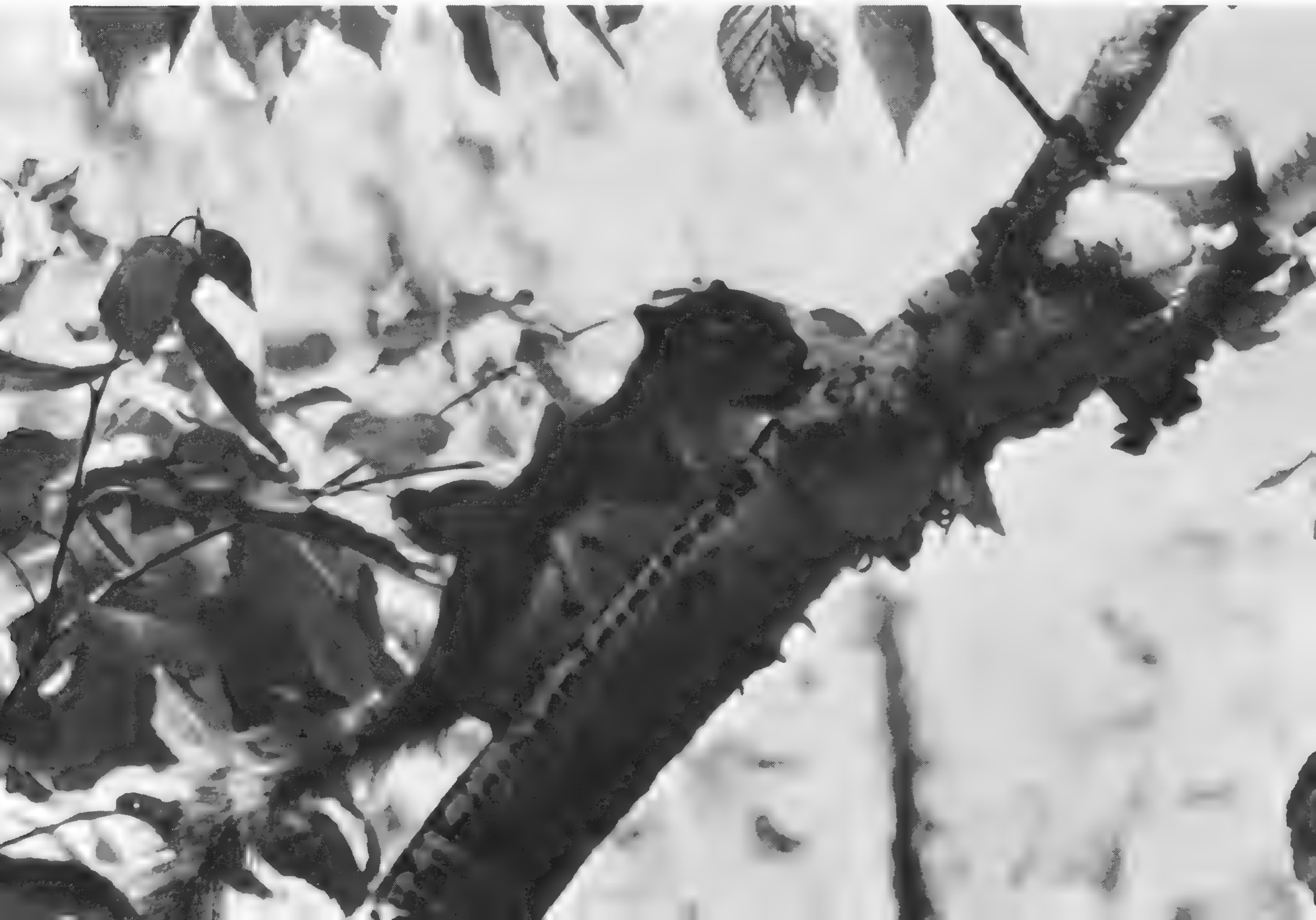


Figure 7 *(above)*. White-breasted Nuthatch feeding on sap from sapsucker drillings.

Figure 8 *(below)*. Red squirrel feeding on sap from sapsucker drillings. Only the uppermost holes are producing sap. The squirrel is a lactating female which later brought her young to the tree.



Mammals at the Trees

Bats. We frequently observed bats at night in all six areas (see Table 3). Several individuals regularly flew about the sapsucker feeding areas, capturing insects that had been attracted to the sap flowing from the trees.

We captured Keen's bat and the little brown bat in the vicinity of Area C3. The bats around Areas A, B, C1, and C2 were larger and may have been forest-dwelling bats (silver-haired, red, or hoary bats). We never captured them.

Bats came regularly to the feeding area all through the night. The earliest that we saw them was 9:12 PM and the latest 4:46 AM. Their behavior followed a definite pattern: two or three instantaneously appeared in the feeding area where they fed for a short time and then left just as suddenly. We could not observe where they went; we presumed they alighted and rested. After a varying period of time one or more bats reappeared and began feeding once more. Their feeding periods ranged from 1.5 to 14 minutes, with a mean of 9 minutes. They repeated this pattern until near dawn when they suddenly vanished.

The only insects we saw the bats capture were moths. Beetles and mayflies, known to be flying near the trees, may have formed part of their diet. The bats captured moths in midair or plucked them from the side of the tree while flying. We heard a *snap* or *smack* when a bat took a large moth, such as a birch underwing, which it often consumed while continuing to patrol back and forth among the trees. We could see the wings of the larger moths, which the bat did not eat, flutter to the ground soon after capture.

TABLE 3

Mammals Associated with Feeding Trees of the Yellow-bellied Sapsucker

Species	*Feeding on insects*	*Feeding on sap*	*Authority*
Vespertilionidae			
Little brown bat (*Myotis lucifugus*)	X		Pers. observ.
Keen's bat (*Myotis keeni*)	X		Pers. observ.
Sciuridae			
Eastern chipmunk (*Tamias striatus*)		X	Kilham, 1964.
Red squirrel (*Tamiasciurus hudsonicus*)	X	X	Hatfield, 1937; Kilham, 1958b; Nickell, 1965; pers. observ.
Northern flying squirrel (*Glaucomys sabrinus*)	X	X	Schmidt, 1931; pers. observ.
Erethizontidae			
Porcupine (*Erethizon dorsatum*)		X	Pers. observ.

Squirrels. Three species of Sciuridae are known to visit sapsucker trees (see Table 3). According to Kilham (1964), an eastern chipmunk in New Hampshire fed on the sap of birch trees drilled by sapsuckers. This animal had to climb a few feet above a man-made girdle on the tree to reach the sapsucker holes. We have no records of chipmunks at sapsucker trees in our study area.

Sap has long been recognized as a portion of the diet of the red squirrel. It usually obtains the sap in the spring from sugar maples (*Acer saccharum*) where the trees have been injured by lightning or wind, or even from holes made by the squirrels themselves. Hatfield (1937:242) first reported red squirrels at sapsucker drillings, and Kilham (1958b:596) repeated some of his observations.

We saw red squirrels at our study areas daily throughout the period of observation (Figure 8). They appeared as early as 5:29 AM and the peak of their morning activity came usually about 6:40 — after the height of the morning activity of the sapsuckers. The sapsuckers had a second peak of activity shortly after the red squirrels had finished their first morning feeding. Throughout the rest of the day the red squirrel activity was much more casual than during the peak morning hours. The animals spent long periods cleaning their fur, gnawing at the holes, and occasionally attempting to catch insects. Often large numbers of flies, bees, and hornets had gathered at the same band of holes where a squirrel was feeding. When noticeably disturbed by the insects, the squirrel covered its nose with its paws and twitched or switched its tail to avoid them.

Usually the squirrel lapped the sap out of the small well present at each hole. It also licked the sap flowing down the side of the tree, and frequently gnawed out spaces between adjacent holes. In this way it obtained food from the sap-soaked bast as well as gaining better access to the holes on later visits. The red squirrels fed from all positions, sometimes standing on an adjacent branch; sometimes even hanging upside-down from the smaller limbs.

The red squirrels' frequent attempts to capture insects were mostly unsuccessful. They often ignored the ants, present on the bark in abundance, but eagerly pursued other insects, especially butterflies when they were present. In this regard the squirrels were opportunists, trying to catch the insects only when they alighted nearby. They occasionally captured cicadas, flies, and butterflies, but avoided hornets, wasps, and bees.

The red squirrel approached the feeding trees from the ground as often as through the tops of the trees. When coming from the ground, red squirrels avoided climbing on the bark of larger birch trunks which they apparently found too slippery. Instead, whenever possible they climbed up on adjacent cedars, spruces, or a thinner birch trunk that they could nearly reach around.

In Area A, at least two red squirrels fed regularly at the drilled trees until about 1 July. After that time at least one lactating female and three young, probably her offspring, used the trees. Neither of the adults, seen prior to 1 July, was noted to be lactating. Similarly, an adult female fed at Area C1 from our first observation and brought her young to the tree at 5:00 AM on 2 July. Eighteen days later the female ceased coming; the young continued to feed there throughout the summer.

We saw northern flying squirrels in feeding trees for the first time anywhere at Area A on the night of 29 July 1963. No doubt they were present before this date because after that time we observed flying squirrels repeatedly at every area. Two or perhaps three individuals were present at most areas, and we saw and heard five individuals at once at Area C1 (Figure 9). We

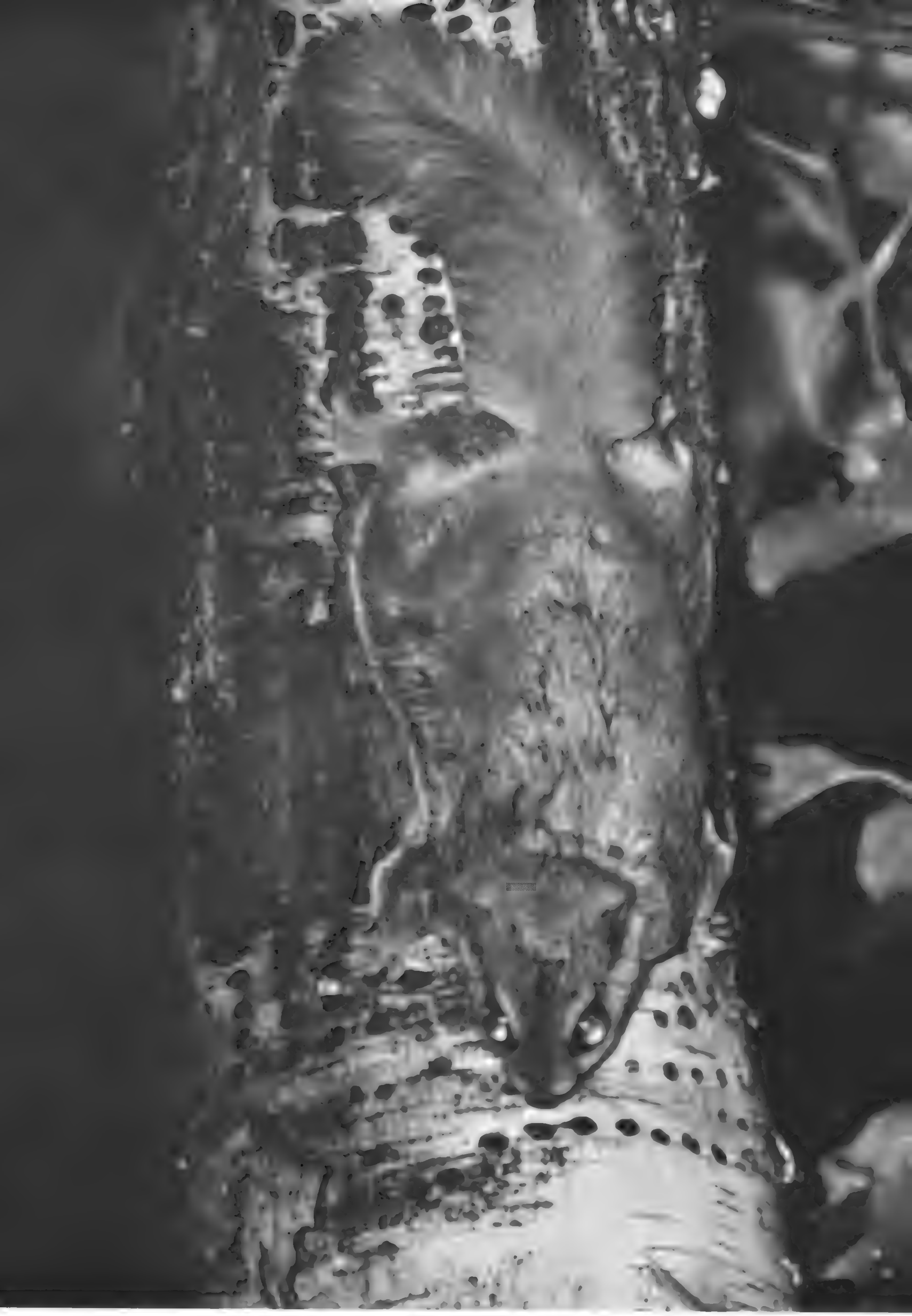


Figure 9. Northern flying squirrel at feeding area of Yellow-bellied Sapsucker.

encountered great difficulty in attempting to follow their movements in the darkness, even though the use of flashlights and infra-red light facilitated our observations.

Schmidt (1931:110) reported collecting moths at a sapsucker tree that was also visited by northern flying squirrels. Seton (1929:390) mentioned that flying squirrels often drowned in the sap buckets of maple-sap collectors. We found no reference to the southern flying squirrel eating sap although it might be expected.

Flying squirrels appeared in the study area about 8: 20 PM, after the sun was down, but while there was still some light. Late in August 1963, one flying squirrel arrived at 7:53 PM. Due to the fact that the red squirrels were sometimes still active when the flying squirrels appeared, it was often difficult to obtain accurate data for the arrival of the flying squirrels. After an initial burst of feeding activity, flying squirrels visited the trees intermittently throughout the night. We observed them in the vicinity of the trees until 4:45 AM.

The flying squirrels showed little fear of a flashlight beamed from the observation platform ten feet away, so long as we did not shine it on them for a long time (Figure 9). Upon prolonged exposure to the light, the squirrel moved around the tree.

When feeding, flying squirrels lapped the sap out of the holes or licked it from the bark and, as Schmidt (*loc. cit.*) noted, they chewed the bark out from between adjacent holes.

Moths, the most abundant night-flying insects at the tree, formed an important food item for the flying squirrels. The squirrels caught the moths most successfully by stalking and pouncing on a moth that had alighted. Occasionally, they captured flying moths with the forefeet, while maintaining a hold on the trees with the hind legs. They ate only the body of the insect, allowing the wings and legs to drop away.

Flying squirrels frequently glided from tree to tree, regularly traversing up to 100 feet. Not uncommonly they struck a branch or a support wire for the blind while in midair and dropped to the ground short of their probable goal. We saw no apparent injury from these mishaps. After landing on the ground, the flying squirrels sometimes ran quickly to a nearby tree, but more often they foraged. Once a flying squirrel landed in a small creek and had to pull itself out before scrambling up a tree. In Area C1, the flying squirrels spent as much as 50-70 per cent of their time on the ground. In climbing to the holes they most often used trees adjacent to the birches and scaled across. However they spent relatively more time on the birches than the red squirrels when traveling up or down trees. This may have been because of their smaller size and lighter weight.

Porcupine. At 4:24 AM on 4 August 1965, a porcupine, present since before the observation began, climbed down from above the holes in Area C2. There were no moths at the holes, but flying squirrels and bats were in the area. After gnawing steadily for a time at the bark around the sapsucker drillings, it descended to the ground and disappeared into the bog.

Summary of Round-the-Clock Activities

Our 250 hours of day and night observations have revealed that sapsucker trees are the scene of practically continuous animal activities. Visiting species during the day are replaced as night approaches by different species. Figure

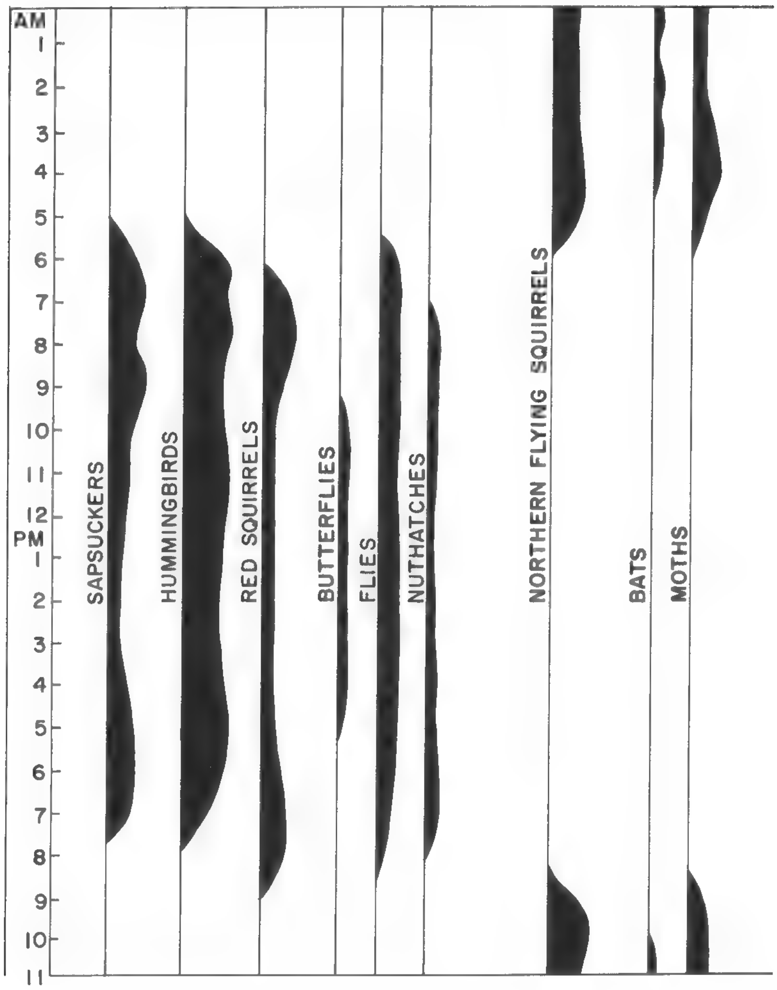


Figure 10. Composite 24-hour chart showing the hourly extent and the intensity of activity of several common visitors to feeding trees of the Yellow-bellied Sapsucker. The width of the activity line for each group of visitors indicates the relative activity index which was obtained by multiplying the number of visits per half-hour by the duration of each visit.

10 summarizes, on a 24-hour chart, the hourly extent and the intensity of activities of several common visitors to feeding trees recorded by us.

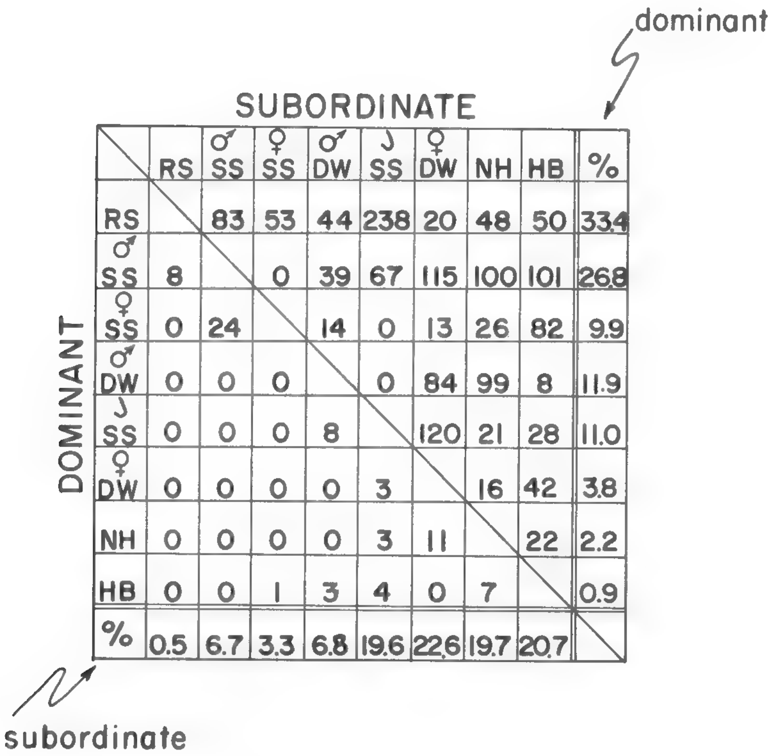
Coactions

The relationship between the sapsucker and most of the animal visitors to the tree was one of facultative commensalism. Each of the visiting species can survive independently of the sapsucker. Only the hummingbird was largely dependent on a diet of liquid food. It established a nearly permanent relationship with the feeding trees throughout the summer. Certain of the predators (bats, hawks, and predatory insects) took advantage of the concentration of the prey at the feeding tree, although they normally might have preyed on the same species elsewhere.

The effect on the commensal species is debatable. Although some male sapsuckers spent much time and energy defending their trees, in no case did we note any effect on the well-being of these birds. The female and juvenile sapsuckers were less aggressive than adult males in defense of the tree. Late in the summer the juveniles persistently displaced other birds from choice feeding locations, but apparently did so with little difficulty.

Since the sap attracts a large number of animals simultaneously, competition between species results in the development of a social hierarchy. In our 250 hours of recording minute-by-minute activities at the feeding trees, we carefully noted instances of interspecific and intersexual dominance. We used two criteria for dominance: (1) If individual A was displaced from the feeding holes, or refused to approach the holes because of the immediate presence of individual B, then we considered individual B dominant, or (2) if animal A continued to feed in the face of aggression from animal B, then we considered individual A the dominant one.

Data were recorded on a chart similar to Figure 11 where the figure at the intersection of two rows represents the number of times an animal in the vertical row was dominant over the animal in the horizontal row. In Figure 11, which summarizes 1,605 intersexual and interspecific conflicts, the most dominant animals are toward the left and top, and more subordinate animals toward the right and bottom. In this way those numbers below the diagonal represent irregular dominance and triangle relationships. The number of times an animal dominated all other species is totaled at the end of the horizontal column for that species. The number of times an animal was subordinate is at the bottom of the vertical column for that species.



dominant

SUBORDINATE

DOMINANT

	RS	♂ SS	♀ SS	♂ DW	J SS	♀ DW	NH	HB	%
RS		83	53	44	238	20	48	50	33.4
♂ SS	8		0	39	67	115	100	101	26.8
♀ SS	0	24		14	0	13	26	82	9.9
♂ DW	0	0	0		0	84	99	8	11.9
J SS	0	0	0	8		120	21	28	11.0
♀ DW	0	0	0	0	3		16	42	3.8
NH	0	0	0	0	3	11		22	2.2
HB	0	0	1	3	4	0	7		0.9
%	0.5	6.7	3.3	6.8	19.6	22.6	19.7	20.7	

subordinate

Figure 11. Summary of 1,605 intersexual and interspecific conflicts in sapsucker feeding areas. The numbers indicate how often each animal in the vertical row dominated each animal in the horizontal row. RS, red squirrel; SS, adult Yellow-bellied Sapsucker; DW, Downy Woodpecker; NH, nuthatch; HB, Ruby-throated Hummingbird; JSS, juvenile Yellow-bellied Sapsucker.

Three definite levels of dominance are evident in Figure 12, based on cumulative totals of the results of all encounters for each species (or sex). The red squirrel showed clear supremacy over all of the other animals. Even though the sapsucker was responsible for social aggregation at the tree, it was subordinate to the red squirrel. Only by repeated attacks, accompanied by raised crown feathers and alarm calls, could the male sapsucker sometimes drive the red squirrel from the holes. Such attacks on the red squirrel largely ceased with the fledging of the young sapsuckers.

Intermediate dominance was found in the male sapsucker, the female sapsucker, and the male Downy Woodpecker. The female sapsucker reacted to other species present at the tree just as the male did, except that she usually lacked the same degree of aggressiveness toward the red squirrel. The differ-

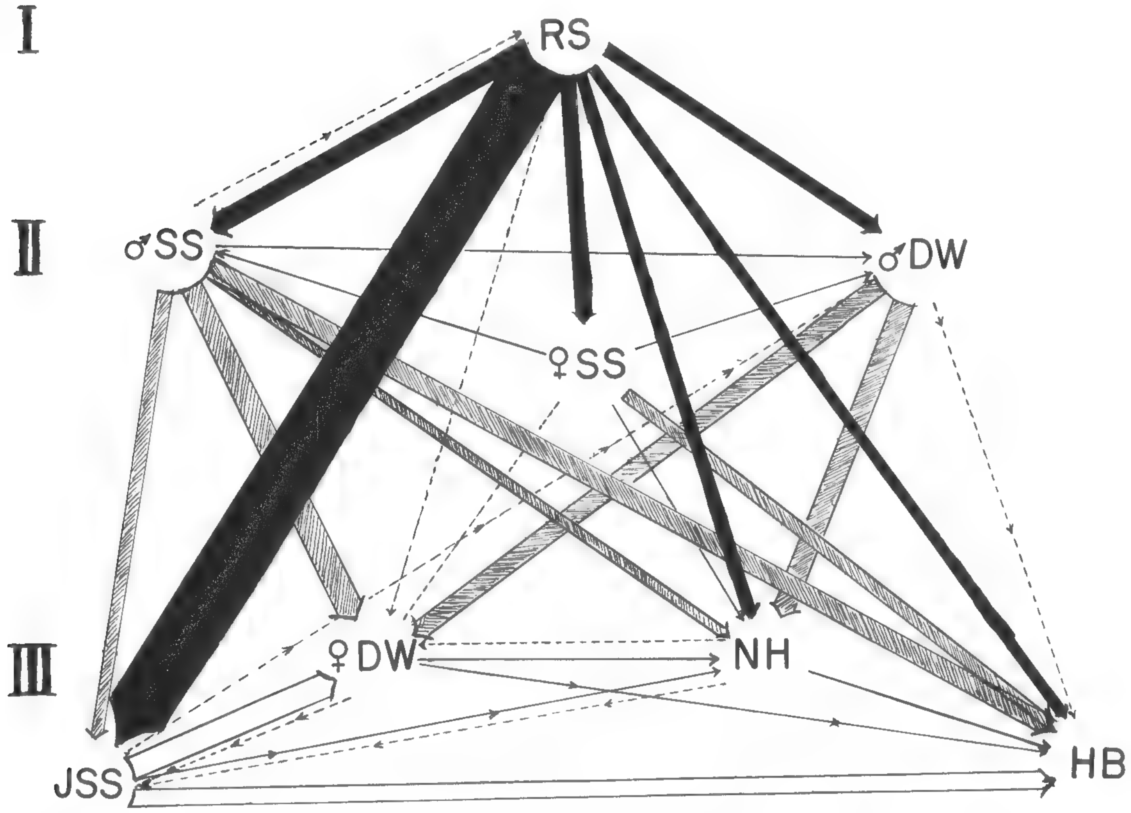


Figure 12. Social hierarchy among the more common vertebrate visitors at two sapsucker trees in Michigan. The width of the arrows and the positioning of the animals is based on the data in Figure 11.

ence observed in male and female Downy Woodpeckers illustrated a probable difference in sexual dominance where the male clearly dominated the female and immatures. This trait in the male was most pronounced when there were a number of Downies at the tree.

Four groups of animals occupied the lowest level in the social hierarchy: the juvenile sapsuckers, the female Downy Woodpecker, the nuthatches, and the hummingbirds. The two species of nuthatches have been grouped in one category here because of the similarity of their behavior. The two species dwell in completely different habitats. The Red-breasted Nuthatch inhabits coniferous bogs and the White-breasted Nuthatch the uplands and lake shores. Since we found sapsucker feeding trees in both bogs and uplands, each species of nuthatch utilized the trees, but we never observed both in one area. The nuthatches, like the Ruby-throated Hummingbird, seemed to dominate another species only when they appeared suddenly around a tree and startled the other animal.

The aggressiveness of the young sapsuckers increased from their first arrival at the tree until late in the summer. In the first few days at the tree they assumed a rather tolerant attitude and were very flighty. They were flushed frequently from the tree, even by members of their own family. Near the end of the summer the young sapsuckers showed more aggressiveness toward other birds and even went out of their way to supplant other birds. This gradual increase in aggressive behavior lifted them from a lower social level in July to a second level by late August. When data from fledging to late August are considered together (as in Figure 11), they occupy an intermediate position.

Thus we have a well-established social hierarchy among the larger and more regular vertebrate visitors to a sapsucker feeding tree. A similar study might define and relate the interactions among the smaller vertebrates, the night visitors, or the insects and their associates at the tree. Our observations indicate that certain of the Vespidae and Bombidae dominate the insect associates at the tree, and may even become so numerous as to pose a formidable nuisance to some of the vertebrates.

Significance of the Feeding Area in the Ecosystem

We might compare the natural situation of sapsucker feeding areas attracting an aggregate of animals to the artificial attraction of birds to a feeder. Both gather a large group of individuals around a concentrated supply of food. Just as individual birds become regular visitors to a backyard feeding station, so do certain animals become regular visitors at the sapsucker feeding area. The daily routine of some animals undoubtedly undergoes a pronounced change upon discovery of the sapsucker feeding area. Where previously an animal might have foraged over a large area, it may quickly concentrate on the sap and/or insects on the sapsucker trees. Since each breeding pair of sapsuckers will have at least one feeding area with up to eight or ten feeding sites, it is obvious that there is a significant effect on the local ecosystem.

Just as a well-stocked backyard feeder sometimes maintains a bird extraseasonally or extralimitally, so does a sapsucker feeding area have a similar effect. Thus, three Baltimore Orioles remained at sapsucker drillings throughout the winter in Norfolk, Virginia (Sykes, 1960), and a Painted Redstart spent several days in winter at a sapsucker feeding area in California (Goodman, 1954). This was the fifth winter record for the state.

Initially, the association of animals at a sapsucker tree might appear as an interesting oddity of nature; but the consistent appearance of records of feeding-tree visitors in the literature, and the regularity of certain of the species at sapsucker trees, indicate a more persistent association.

We found that the presence of a sapsucker feeding area invariably heralded the presence of hummingbirds, red squirrels, flying squirrels, butterflies, hornets, and ants—to name a few. In good habitat for nesting sapsuckers, two or three pairs per acre is not unusual, and the local impact of their presence becomes pronounced.

Sapsuckers obviously harm individual trees. Extensive drilling kills birches in two to three years. The effect of birch-killing on the forest is probably not significant. However, when in migration in the middle and southern states, large numbers of sapsuckers sometimes congregate in orchards and cause significant damage.

In this paper we have largely ignored the micro-organisms that are also regularly associated with sapsucker feeding trees. We have noticed fungi (including yeasts), nematodes, and larval insects (including *Drosophila*) in the frothing sap at some holes. Further study will probably show interrelationships that include these organisms and affect the larger visitors. For example, it is well known that sap undergoing yeast fermentation frequently becomes high enough in alcohol content to cause a sapsucker to become inebriated.

Summary

From 1963 through 1965 we studied the summer feeding areas of six pairs of Yellow-bellied Sapsuckers (*Sphyrapicus varius*) in northern Lower Michigan. The sapsuckers fed on phloem sap obtained in different ways and from different types of trees, varying with the

season. Animal visitors—insects, birds, and mammals—were consistently associated with sapsucker feeding trees, attracted to the flowing sap and/or insect life at the trees. Butterflies, moths, flies, hornets, and bees were the most numerous insect groups. Birds totaling 20 species appeared at the feeding trees. The Ruby-throated Hummingbird was the most numerous of all birds, including the sapsucker itself. Segregation of the sexes of hummingbirds to specific feeding areas was observed. A female hummingbird built a nest within fifty feet of a feeding tree, and its activities centered about both the tree and nest. Bats, northern flying squirrels, and red squirrels were always associated with sapsucker trees. In studying the round-the-clock activities and interrelationships of all the animals visiting the sapsucker trees, we found that a prominent social hierarchy developed among the more frequent visitors and that the summer feeding trees of Yellow-bellied Sapsuckers have a significant effect on the local ecosystem.

Acknowledgments

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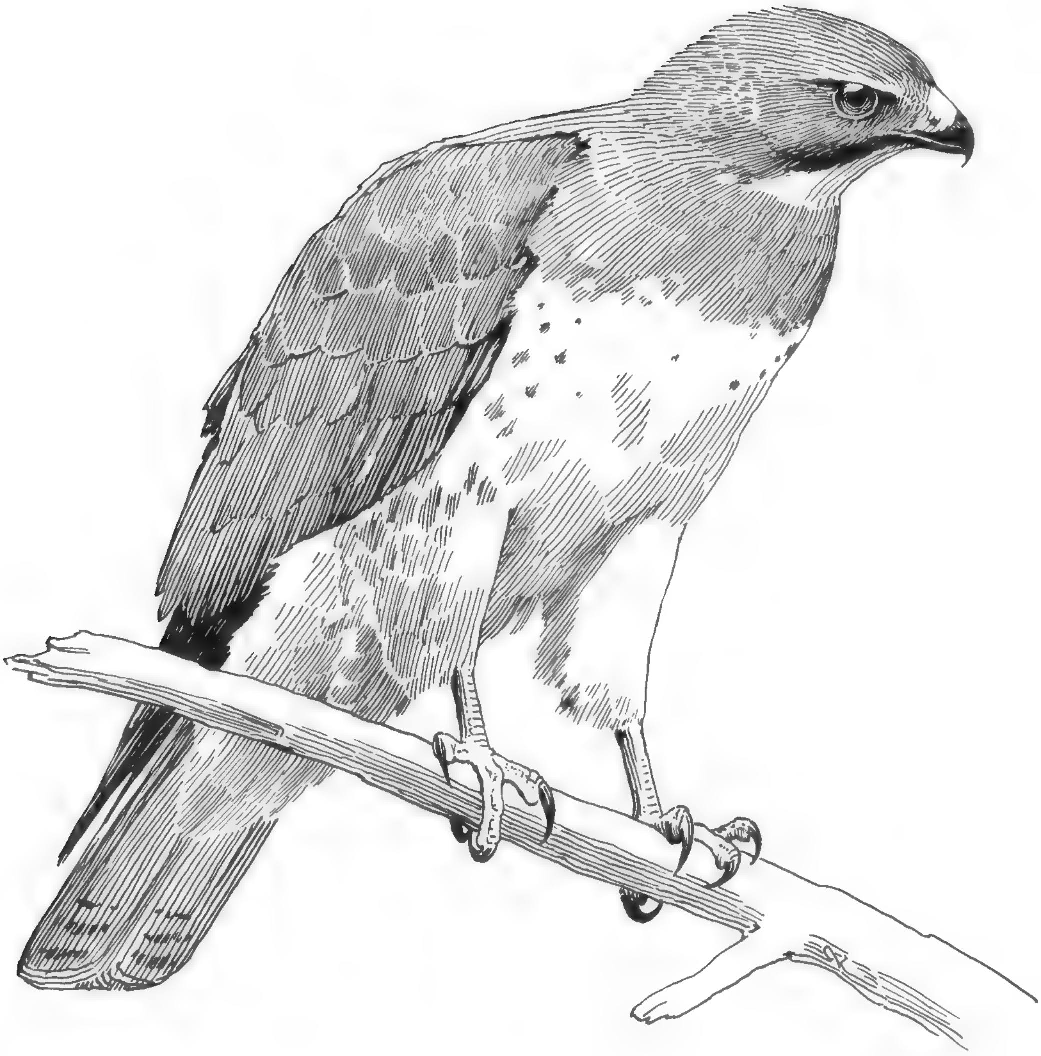


Swainson's Hawk, *Buteo swainsoni*. Drawing by George Miksch Sutton.

THE PECKING RESPONSES OF PEAFOWL CHICKS

William C. Dilger and J. Cherrill Wallen

Many precocial young birds have an innate pecking response, which they direct at small objects in the environment and which presumably insures the ingestion of food. According to C. L. Morgan and H. Poulsen, as cited in Kruijt (1964:13), young chicks of the genus *Gallus* gradually learn to reduce pecking at inedible objects but this never entirely ceases. R. L. Fantz, as cited in Kruijt *(loc. cit.)*, found that chicks of the Domestic Fowl (*Gallus gallus*) have a preference for round rather than angular objects. Curtius (1954), however, noted no significant shape preferences among the young of Domestic Fowl, Domestic Turkeys (*Meleagris gallopavo*), and Lapwings (*Vanellus vanellus*) when she presented them with circles, squares, triangles, crosses, rods, and ellipses of equal area.

Where responses to sizes of objects have been tested, young birds show a definite preference. For example, Curtius (*loc. cit.*) found that the young birds she studied preferred objects of the following sizes: Domestic Fowl to 2.5 millimeters; Turkey, 5 mm; and Lapwing, 1 mm.

The evidence for color preferences is somewhat contradictory. Kear (1964) tested the color preferences of many species of anatids (waterfowl) and a few other birds including three species of phasianids: Ring-necked Pheasant (*Phasianus colchicus*), Bobwhite (*Colinus virginianus*), and Gray or Hungarian Partridge (*Perdix perdix*). All of these anatids and phasianids preferred green, with their pecking responses falling off toward both yellow and blue. Hess (1956), testing color preference in Domestic Fowl chicks and ducklings of the domesticated Mallard *(Anas platyrhynchos)*, found that the chicks had a bimodal preference with peaks in the orange and the blue regions of the spectrum. The ducklings had but one peak in the yellowish-green to green region.

"Contrast" has been stated as being one of the features stimulating the pecking response; and certainly, if the object failed to contrast at all with its background, it would not be pecked. On the other hand, birds may not always prefer maximum contrast to lesser contrasts. Curtius (*loc. cit.*) found, for example, that when chicks were offered various gray models against gray backgrounds they preferred the lesser contrasts.

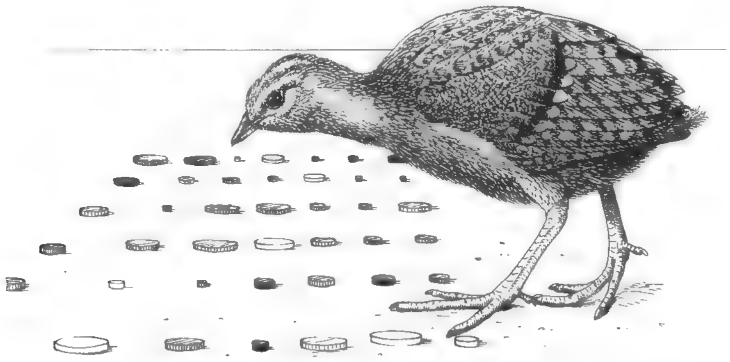
The differences in testing procedures, the relatively small numbers of species tested, and the contradictory results obtained indicate a clear need for further systematic investigations of this sort. We have attempted to test the color, size, and contrast preferences of four young Indian Peafowl (*Pavo cristatus*) and hope to test other species as they become available.

Materials and Methods

Through the kindness of Mrs. Roy H. Park of Ithaca, we obtained on two occasions several peafowl eggs which we placed in an incubator. Three chicks (Birds 1, 2, and 3) hatched from the first batch and one chick (Bird 4) hatched two weeks later from the second. We tested Birds 1, 2, and 3 for the first time when they were less than 24 hours old, and Bird 4 for the first time when about 72 hours old.

We cast the test objects in plaster of Paris from Plastelina molds. The objects were 3 mm high, circular, and 2, 4, 6, 8, 10, 12, and 14 mm in diameter. For backgrounds we used sheets of construction paper, 24 by 36 inches, of different colors: red, yellow, green, blue, black, and white. We painted the plaster objects with opaque water colors, matching as closely as possible the colors of the various backgrounds. To each background sheet we glued 42 objects of seven sizes in six colors, spaced evenly within a 42-square-inch area centered on the sheet. We distributed sizes and colors of the test objects at random but arranged them the same way on each sheet.

We presented the prepared sheets in a shallow wooden tray within which they fitted closely. The sides of the tray were 3.5 inches high and left unpainted. We varied at random the edge of the test pattern on which the birds were placed each day; we also varied randomly the order of presentation of the backgrounds.



Each day we paired two of Birds 1, 2, and 3 at random and tested them together; the odd bird we tested separately. The birds were allowed five minutes on each background. If they did not start pecking immediately but began during this period, we retimed them for five minutes from the first peck. If they failed to peck, we removed them at the end of five minutes. We tested each pair and single bird in turn on a single background before presenting them with a new background, and we always made certain to test all three birds on all six backgrounds each day. We continued testing Birds 1, 2, and 3 for 13 days, after which we tested a different one each day with Bird 4.

Our method for testing Bird 4 was similar to that for testing Birds 1, 2, and 3. For three days we tested Bird 4 alone. For seven days after that, feeling that its being by itself might adversely affect its performance, we tested Bird 4 with one of the older birds.

Results

We recorded a total of 975 pecks. The pecking response fell off rather rapidly; the majority of pecks were made during the first three days of testing. However, although pecking did reach very low levels, it never ceased throughout the entire period.

Figure 1 shows the number of pecks that we recorded for each of the four birds during the first nine days of testing. Note that Birds 2 and 3, which were somewhat younger than Birds 1 and 4 when first tested, had a lower initial pecking response. This may have been because Birds 2 and 3, being younger, had not yet achieved as high a degree of maturation as had the other two.

Like *Gallus* chicks, these birds seemed to learn rather rapidly to reduce their pecking of inedible objects. The drop in pecking responses occurred after the second day of testing regardless of the absolute ages of the birds.

As indicated by our data, summarized in Figure 2, our peafowl chicks preferred to peck objects that measured 2 mm. Their responses rapidly diminished with increasing size of objects until they encountered objects measuring 12 and 14 mm. We can explain this apparent discrepancy. The edges of the larger objects tended to have minute imperfections such as air bubbles. In almost every case our notes reveal that the birds actually seemed to be pecking at these imperfections rather than at the object itself. Figure 2 shows the sizes of objects preferred computed as percentages of total pecks.

The preferences of our chicks for certain colors of objects were clear cut. The birds pecked at black and white the most and about equally. They pecked less frequently at objects toward the red end of the spectrum; thus they preferred blue over green, green over yellow, and yellow over red. Figure 3 shows their preferences for colors of objects expressed as percentages of total pecks; Figure 4 gives the details of the colored objects they preferred in association with the various sizes and backgrounds.

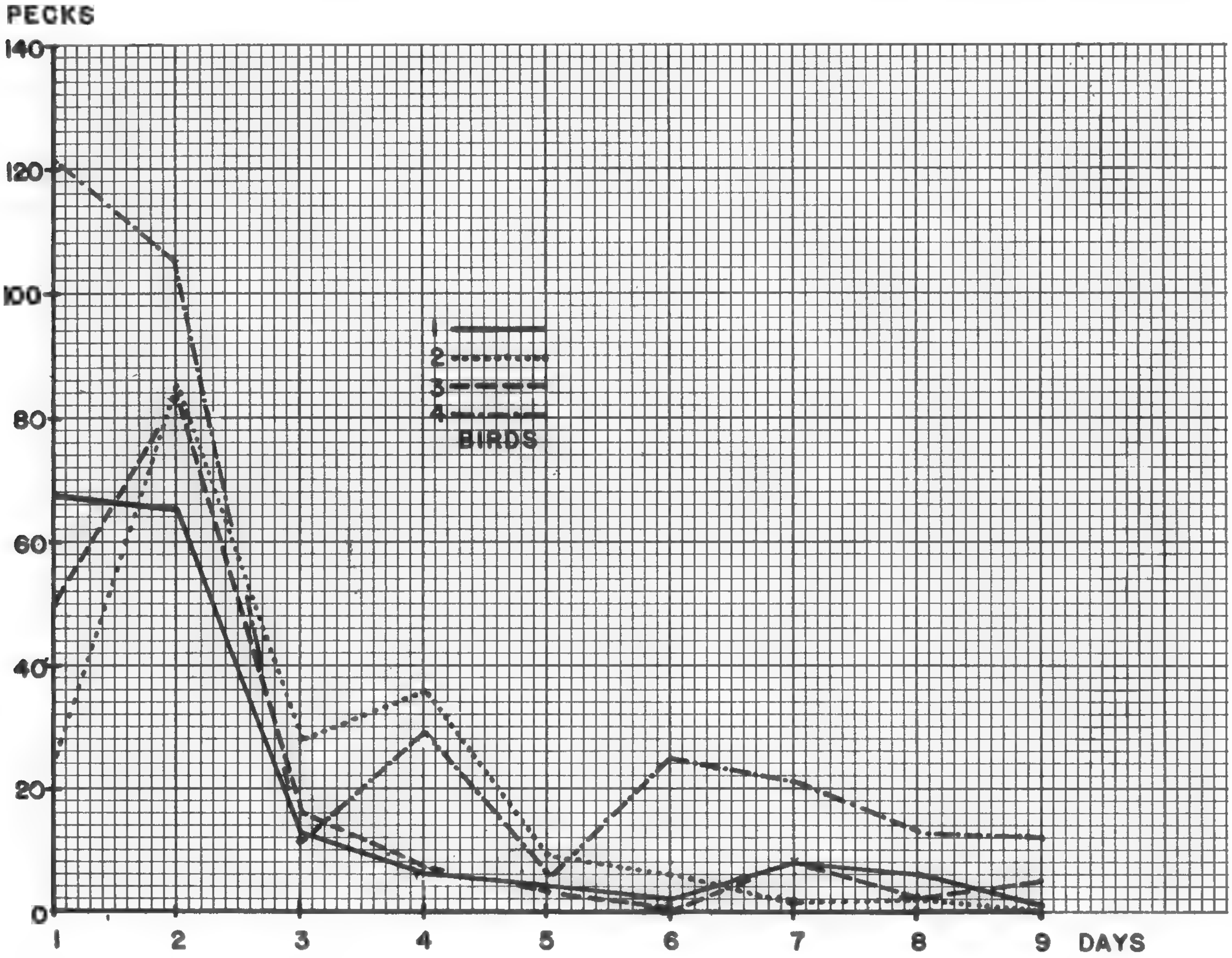


Figure 1. The number of pecks recorded for each of four Indian Peafowl chicks during the 30-minute test period of the first nine days of testing.

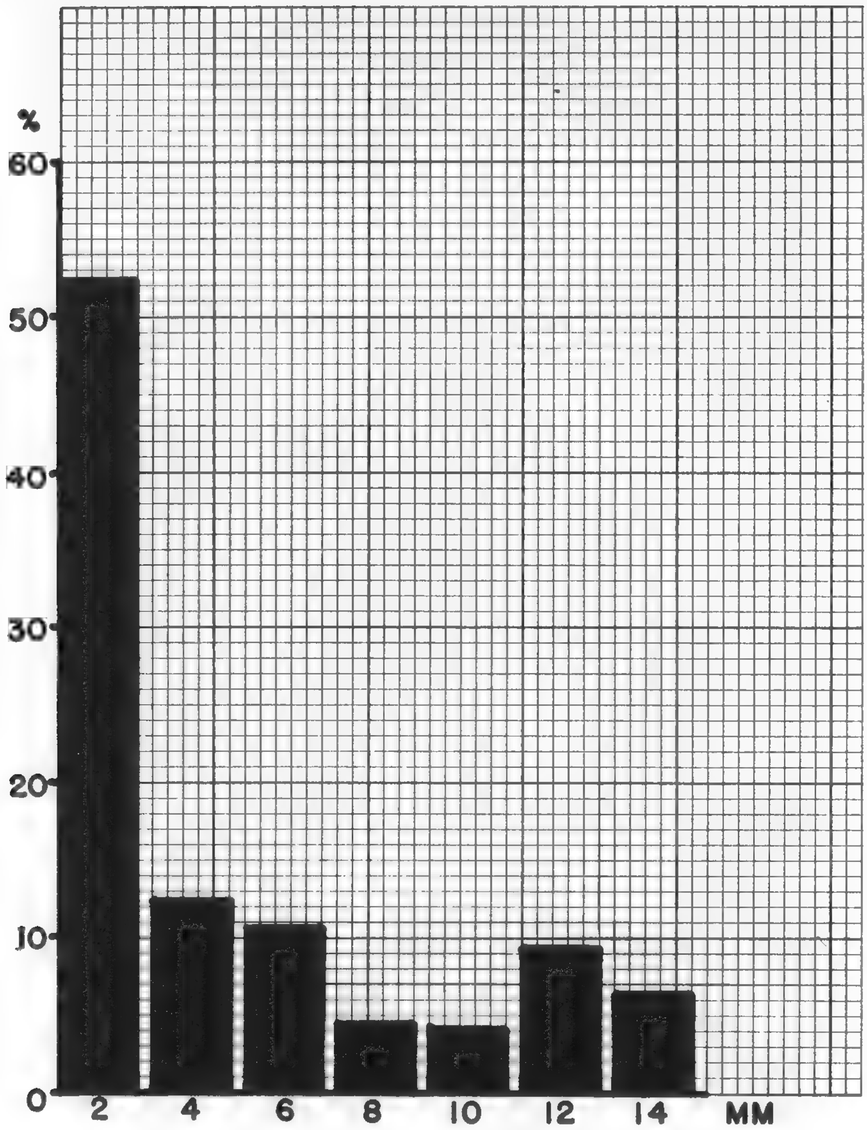


Figure 2. The number of pecks, expressed as percentages of total pecks, directed by four Indian Peafowl chicks at each of seven sizes of objects.

The background-object associations present some perplexing data. In general, the backgrounds preferred are the reciprocal of the colored objects preferred except that black remained rather high. Figure 5 gives the details of background preferences for each color object and for all sizes that we presented. Figure 6 shows the total number of pecks directed at objects on each of the six backgrounds. The high value for the red background is almost entirely due to a penchant of the chicks for pecking black against red and, to a lesser degree, red against red. The chicks pecked least at blue and green against red, and they preferred white against yellow more than against any other background. They pecked little at other colors against yellow and avoided blue especially. Seldom did the chicks peck at red and yellow against the green background, although they often chose blue and white. Against the blue background they preferred green, blue, and black; while against the black background they preferred blue and pecked at green, black, and white only moderately. The chicks seldom pecked any colors against the white background. White objects against white they pecked least and red objects against white most. They pecked at black against white as often as they did yellow against white.

Discussion

These data pose some interesting questions. First of all, it must be assumed that the pecking response and the stimuli eliciting and directing it are adaptive. The pecking response must be organized for each species in such a way that its employment insures the maximum probability of edible objects being ingested, and inedible or dangerous objects not being ingested.

Young peafowl are quite omnivorous. They eat a variety of small seeds, tender leaves, and almost any animals large enough to notice and small enough to ingest. Although red and yellow food items are relatively rare, there is an increasing probability that food objects may be found in the yellow-green to green-blue portion of the spectrum. Beyond the green-blue into the blue-green, blue, and violet portions of the spectrum there are decreasing probabilities of finding food. Kear (1964) found that the color preferences of her anatids and phasianids were centered around green and fell off on both sides toward the blue and the yellow. However, our peafowl showed an increasing preference from yellow to green to blue (see Figure 3). It may be that peafowl are adapted to peck at objects reflecting the shorter wave lengths, perhaps beginning around the yellow-green portion of the spectrum and continuing to the end of the visible portion. This would be safe enough from an adaptive standpoint because relatively few objects in the wild reflect portions of the spectrum much beyond blue-green and few of those that do would require a response of any kind, being neither edible nor harmful. Thus, perhaps there have been no selective pressures for a cut-off point in sensitivity toward the shorter end of the spectrum. The blue end of the spectrum might even be a kind of "super normal" stimulus for this species if its members are adapted to peck at objects reflecting the shorter wave lengths.

Since Curtius (1954) found that Domestic Turkeys preferred 5 mm objects, we felt that our testing range from 2 mm to 14 mm in increments of 2 mm probably embraced the preferred size for peafowl. It is obvious now that this was a poor assumption. The peafowl preferred a size of 2 mm which was perhaps somewhat smaller than Curtius' Domestic Fowl chicks preferred

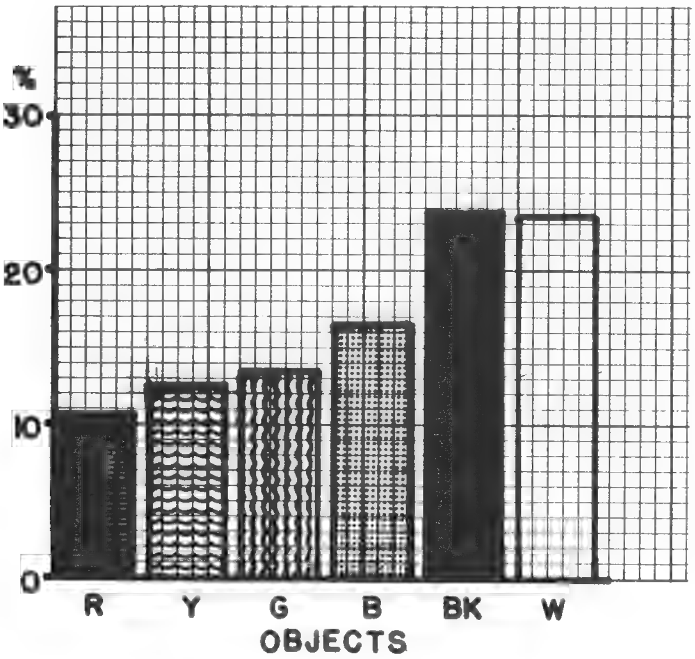


Figure 3. The number of pecks, expressed as percentages of total pecks, directed by four Indian Peafowl chicks at each of six colors of objects. R, red; Y, yellow; G, green; B, blue; BK, black; and W, white.

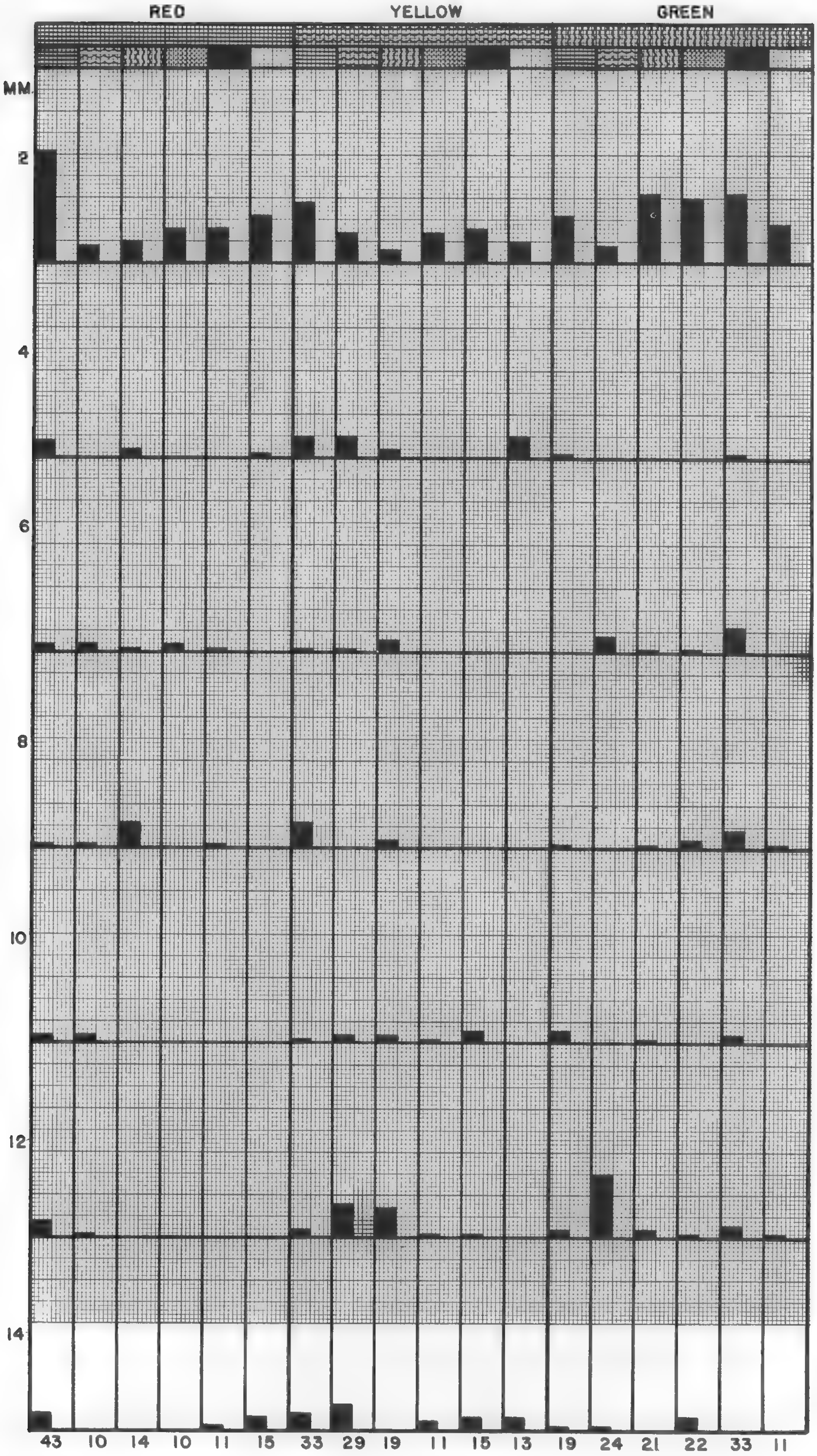
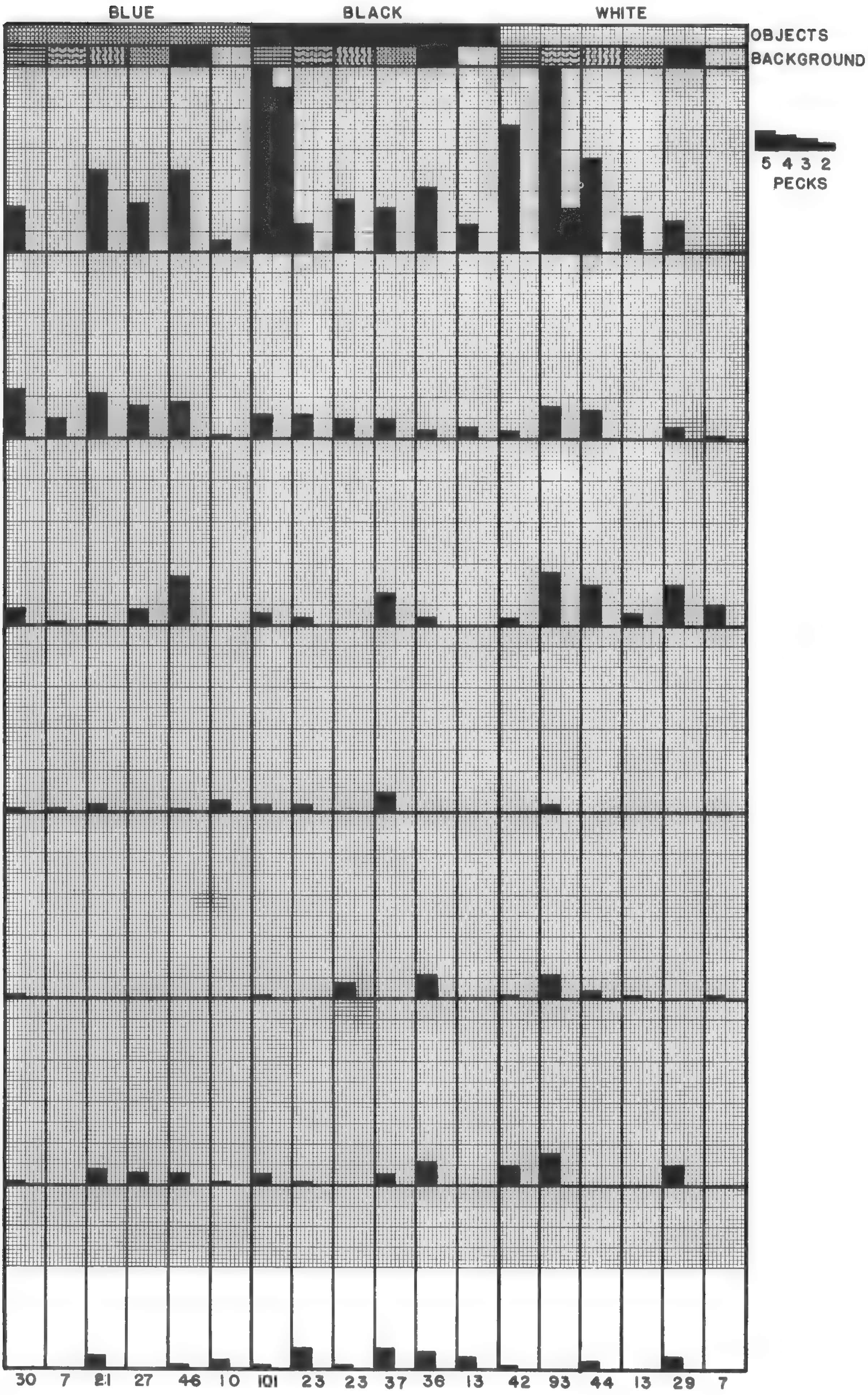


Figure 4. Total numbers of pecks by four Indian Peafowl chicks at six colors of objects in association with the various sizes and backgrounds. The numbers along the bottom represent total pecks for each vertical column.


BLUE
BLACK
WHITE
OBJECTS
BACKGROUND
5 4 3 2
PECKS
30 7 21 27 46 10 101 23 23 37 36 13 42 93 44 13 29 7

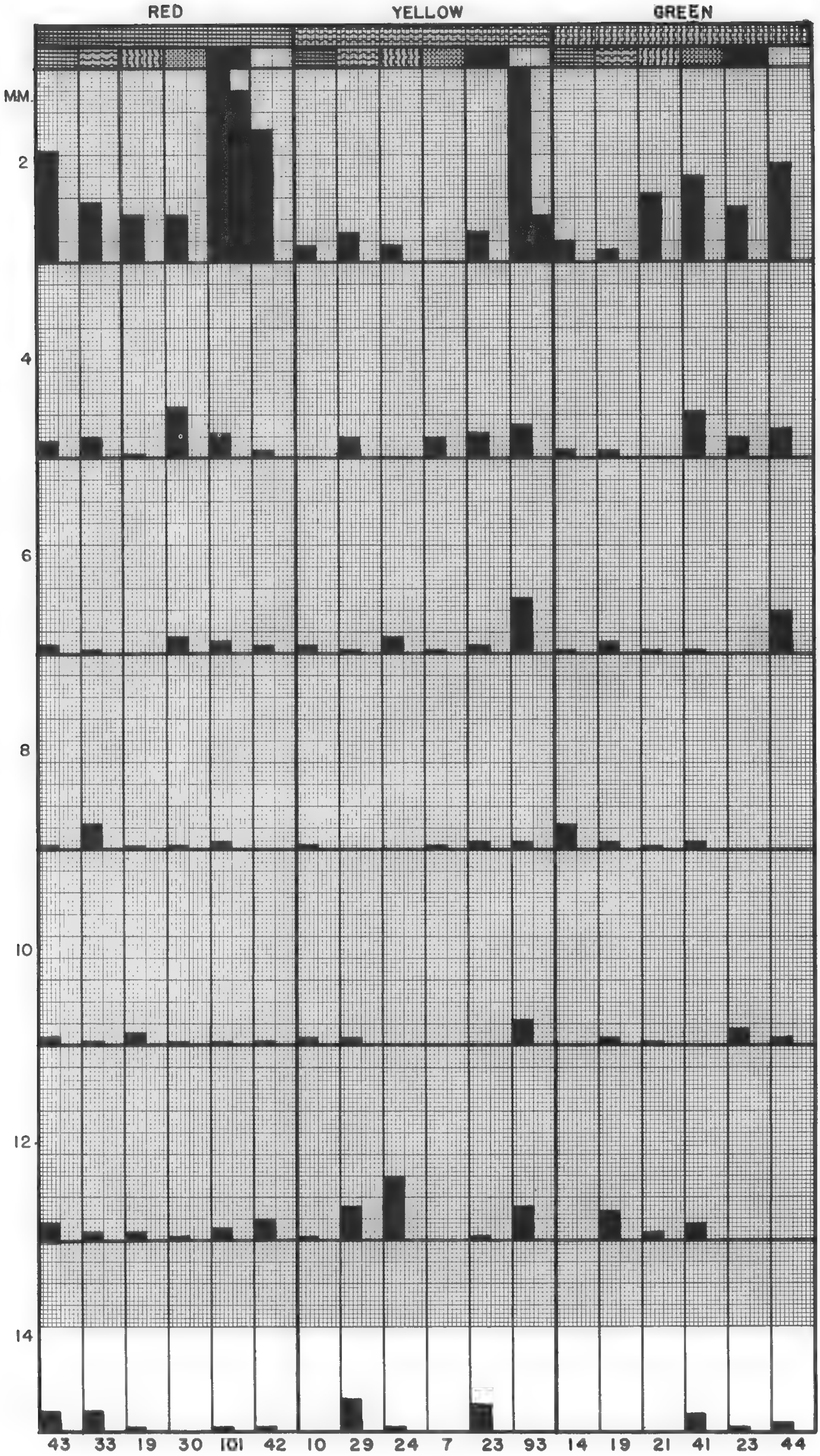
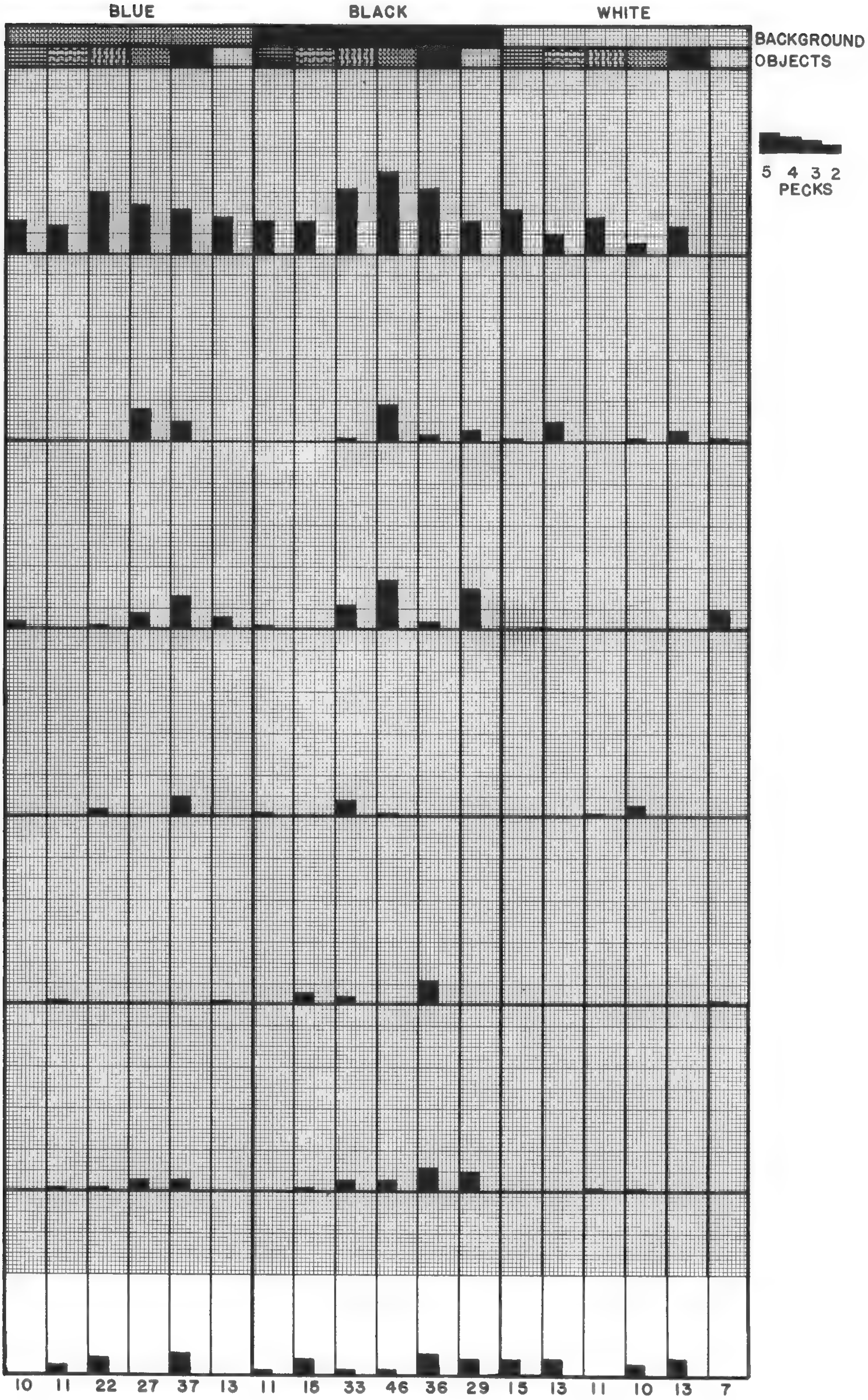


Figure 5. Total numbers of pecks by four Indian Peafowl chicks at the various sizes and colors of objects against each of six colors of backgrounds. The numbers along the bottom represent total pecks for each vertical column.


BLUE
BLACK
WHITE
BACKGROUND
OBJECTS
5 4 3 2
PECKS
10 11 22 27 37 13 11 15 33 46 36 29 15 13 11 10 13 7

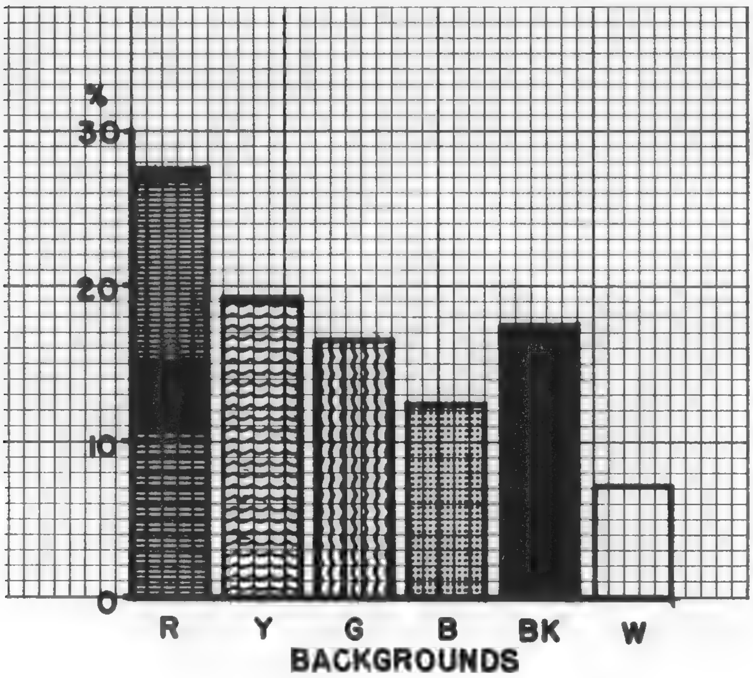


Figure 6. The number of pecks, expressed as percentages of total pecks, directed by four Indian Peafowl chicks at all objects on each of six backgrounds. R, red; Y, yellow; G, green; B, blue; BK, black; and W, white.

(to 2.5 mm) and much smaller than her turkeys preferred. Curtius felt that the size of objects which her three species preferred reflected differences in the sizes of their bills. In view of our findings, this cannot be the only reason for size preferences and we cannot offer any possible explanation for this seeming discrepancy. It would be helpful if we knew more about the food taken by young Domestic Turkeys and Indian Peafowl. Both species are omnivorous, feeding on a large variety of animal and plant food. Both are about the same size, the newly-hatched peafowl being slightly larger.

The relationships between colors of objects and colors of backgrounds present some of the most puzzling situations. If maximum contrast in brightness were important, then black on white or white on black would be preferred. The peafowl preferred black and white objects but not against backgrounds offering these maximum contrasts. Instead, they favored black against red and white against yellow. It is somewhat puzzling why they pecked so often at black against red. It may be that they are relatively insensitive to the red end of the spectrum and that black therefore appears relatively inconspicuous against red. As might be expected, they rarely pecked at white against white. If maximum contrast in hue were important, the birds would peck the colors on those backgrounds offering the most contrast — e.g., red-green, yellow-blue combinations — but this did not happen. Such combinations consistently attracted low numbers of pecks. These colors were more often pecked against backgrounds of the same color.

An examination of Figures 4 and 6 reveals that the chicks preferred combinations of objects and backgrounds offering medium rather than maximum or minimum contrasts in both hue and brightness. It is probably more usual in the wild for edible objects to give medium contrasts with the background. It might be that maximum contrasts are somewhat inhibiting or possibly even somewhat frightening.

Summary

The pecking responses of four young Indian Peafowl were tested to determine their preferences for size and color of circular objects on variously colored backgrounds. The birds clearly preferred the size of 2 mm when given a simultaneous choice of objects ranging in size from 2 to 14 mm, presented in a variety of color-background combinations. They pecked black and white more than red, yellow, green, or blue. Red they pecked the least, yellow more, green even more, and blue most often after black and white. They chose object-background associations with medium contrasts over associations with maximum or minimum contrasts. The data obtained suggest that the amount of experience acquired by young peafowl may be more important than absolute age in their rather rapid learning not to peck inedible objects.

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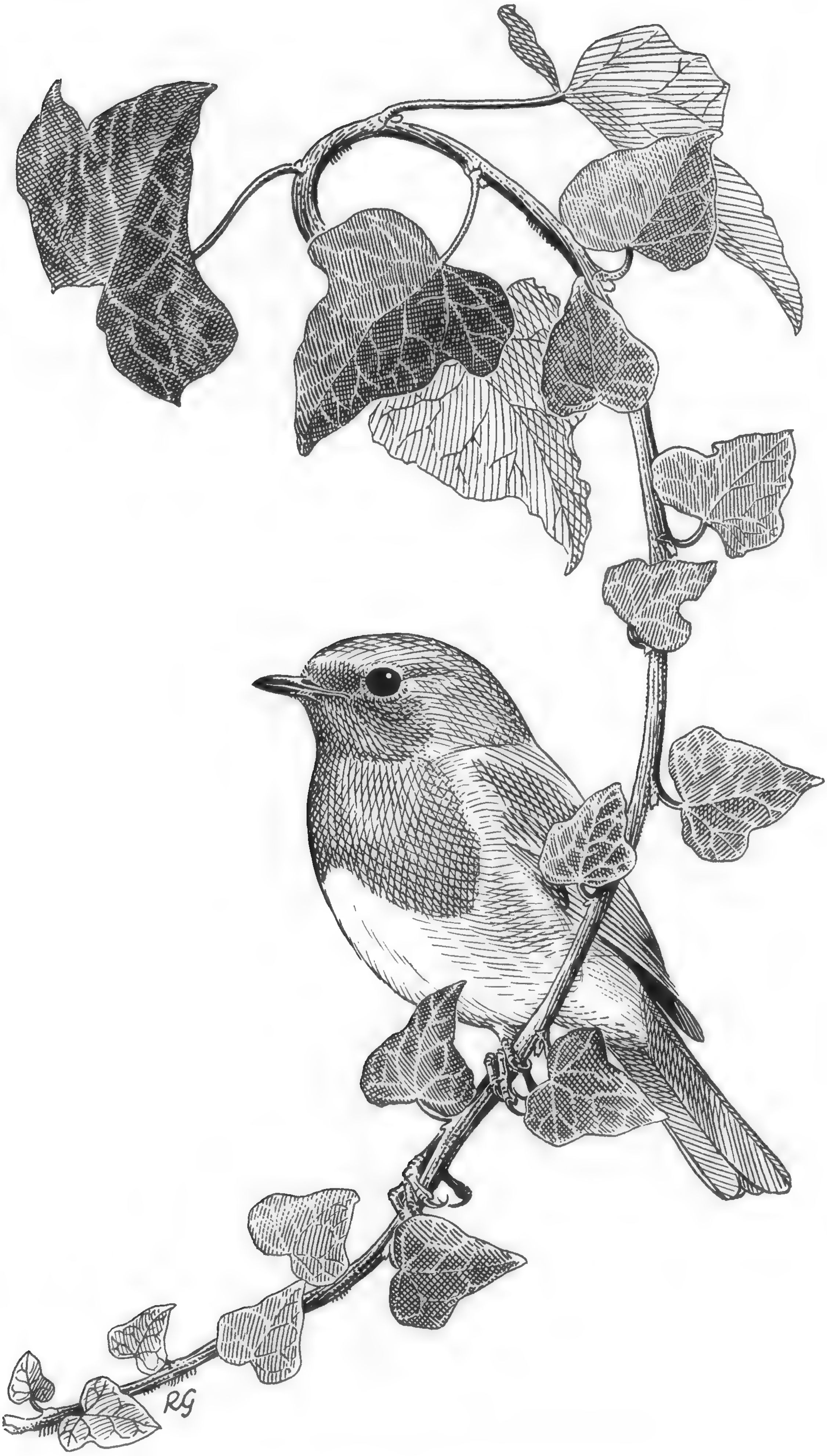

Robin, *Erithacus rubecula*. Drawing by Robert Gillmor.

REGIONAL VARIATION IN THE SONG OF THE CAROLINA CHICKADEE

RODMAN WARD

In this investigation I have considered: (1) the degree of consistency and variation in the song of one species of bird within certain restricted areas; (2) the nature and extent of the variation in the song of the species between the different areas; and (3) the correlation of my data with factors, suggested in the literature as influencing the stereotypy or diversity in song and the development of localized dialects.

The Carolina Chickadee (*Parus carolinensis*) became the subject for this study because it is generally common within its range, easily approached, strongly sedentary, and—most important of all—because the structure of its song is rather simple and more readily comprehended by the human ear than the songs of most species. A tape recorder and a sound spectrograph made possible an objective approach. A statistical analysis of the data avoided subjectively based conclusions and de-emphasized aberrations among individual birds.

From 22 March to 28 May 1963, 13 March to 16 May 1964, and 30 March to 20 May 1965, my wife and I recorded songs of the Carolina Chickadee from close to the northern limit of its range (in Pennsylvania and New Jersey) to about the southern limit (in Florida), along the Atlantic seaboard, and in western Florida. We collected 2,934 songs from 140 birds. I made spectrograms of 227 songs of 118 birds. In addition, we recorded songs of Black-capped Chickadees (*P. atricapillus*) in two areas, northeastern Pennsylvania and Massachusetts, both well outside the range of the Carolina Chickadee. We also recorded chickadee songs in areas (Pennsylvania and Virginia) so close to the common border of the ranges of the two species that we questioned species identification and possible hybridization. I ignore here the songs of the Black-capped Chickadee and the borderline birds except as they provide a background for the analysis of the song of the Carolina Chickadee.

One hundred and thirty of the Carolina Chickadees from which we recorded 2,706 songs were concentrated in nine regions, each ecologically and spatially coherent and each well separated from the others. Two hundred and twenty-eight songs from the remaining 10 birds are excluded from our consideration because the numbers are too small and too geographically diverse to be representative.

In determining the regional characteristics, I considered all songs collected in each of the nine regions as a group and present the data obtained from the application of six parameters, selected as being appropriate to chickadee song. To avoid distortion resulting from the different sizes of the regional samples, any figures, given for all birds in the combined regions, are the means of the regional figures.

Equipment and Methods

We used a Nagra III recorder at a tape speed of 15 inches per second through an AKG dynamic microphone in a 24-inch aluminum parabolic reflector with an eight-inch focal length. Since concentrated experience with one species develops an appreciation of sound level, we seldom needed ear phones. And here I acknowledge my wife who was an invaluable assistant to me in the field, as her ability to use her eyes and ears and to remember what she sees and hears is far superior to mine.

I carried the recording equipment, including the parabola and microphone, slung from my shoulders. A microphone on a tripod might have produced recordings with less extraneous noise, but the extra weight would have made us less mobile, less able to approach and follow a bird. The emphasis was on obtaining a quantity of songs.

Although we became very sensitive to even the least audible of chickadee call notes or to the faint sound of a distant song, we found the broadcast of a pre-recorded song from a second tape recorder very useful in arousing a quiet bird to sing and, if our broadcast was well within its territory, in attracting it closer to us. Because high quality reproduction of song is not necessary in attracting a chickadee, we broadcast from a very inexpensive model for two weeks in 1964—until it broke down—and from an Uher 4000-Report-S in 1965. I shall discuss later the possibility of such broadcasts influencing the form of the reply.

The sound spectrograms were made on a Kay Electric Company Sona-Graph, using the narrow band filter except for a few cases where the less effective representation of short duration was a handicap in understanding a note—for example, a very steep slur or glissando. The narrow band filter provides a better determination of frequencies and any loss of accuracy in representing duration (a constant amounting to approximately 0.02 second) is unimportant in a comparison of durations and thus ignored in the statistics. I attempted no greater accuracy in measuring the spectrographic traces than to 100 cycles per second in frequencies and 0.01 second in duration. To study some unusual songs I made spectrograms at one-half normal tape speed.

Definitions

Song and Note. — The "song" of the Carolina Chickadee is described by Saunders (1951) as the "sweet, whistled notes" and by Brewer (1961) as "typically four-noted" and excludes the less musical vocalizations, such as *tsick-a-dee-dee,* commonly designated as calls. The normal song as I define it here consists of four whistled notes of approximately equal duration, the first and third high, the second and fourth low — HLHL.

A "note," according to Mulligan (1963), is a "sound producing a continuous trace on the sound spectrograph." In other words, a note is a sound separated from other sounds by a period of silence or, in a few cases where there might be a slight temporal overlap, a sound set apart from another by a clear separation of frequencies. A song, in the specific sense, is a series of notes (from one to 12 in our recordings) with time separations up to but not exceeding about 0.15 second. Since the minimum time between two songs is almost invariably two seconds, we had no difficulty in discerning the separation of two songs.

We recorded only songs from the immediate pre-nesting period into the nestling-feeding period when the birds were strongly territorial. At the same time we observed such related matters as hole excavation, territorial dispute (including the birds' active search for and answer to the unseen rival in our tape recorder), copulation, incompleted egg-laying, brooding, nestling-feeding, and nest-cleaning. Therefore, we assume that all our recordings were of mature birds giving advertising or territorial song.

Region. — A "region" refers to one of nine specific areas from each of which all recorded songs constitute a sample. Each region has a consistent ecology and in each of them all of the birds seem to be subject to similar competitive influences.

I shall describe later the parameters used in the measurement of the songs.

Influence of Song on the Form of Reply

I do not believe that the form of a song which incites a territory-defending Carolina Chickadee to answer—whether it be from a neighbor, an invading bird, or a tape recorder—has more than a minimal effect on the form of the reply. In one or two instances we noted that a bird would start its reply with the same song form used by its rival, but would quickly convert to a series in a different, and presumably its own, favored pattern. In many cases, two birds on adjoining territories, engaged in counter-singing, each produced its own different form of song.

The most convincing evidence—that every bird is strongly predisposed to sing in his own fashion and is not diverted by any different style he hears—appeared in 1965 when we broadcast two series of Carolina Chickadee songs during the entire season. These songs, recorded in New Castle County, Delaware, and Beaufort County, South Carolina, were typically four-noted and conformed in all respects to what was presumed to be, and has been found to be, the normal song of the Carolina Chickadee. We used this tape in several regions including Regions 4 and 6. Yet the songs we recorded in Regions 4 and 6 were among the most distinctively abnormal of all.

Regions and Regional Distribution of Data

The maps, Figure 1, show eight of the nine regions. Region 7, on Port Royal, Helena, and Ladies Islands within 10 miles south and east of Beaufort, South Carolina, is omitted.

The regions include recording locations in counties as listed below. The letters to the right of the county names appear on the maps (e.g., PC). The addition of a number to the letters designates an individual bird (PC1). The addition of a hyphen and number designates a particular song of that bird (PC1-1).

Region 1	Burlington, New Jersey	JB
	Ocean, New Jersey	JO
Region 2	Chester, Pennsylvania	PC
	Lancaster, Pennsylvania	PL
	New Castle, Delaware	DN
Region 3	Sussex, Delaware	DS
	Wicomico, Maryland	MWi
	Worcester, Maryland	MW

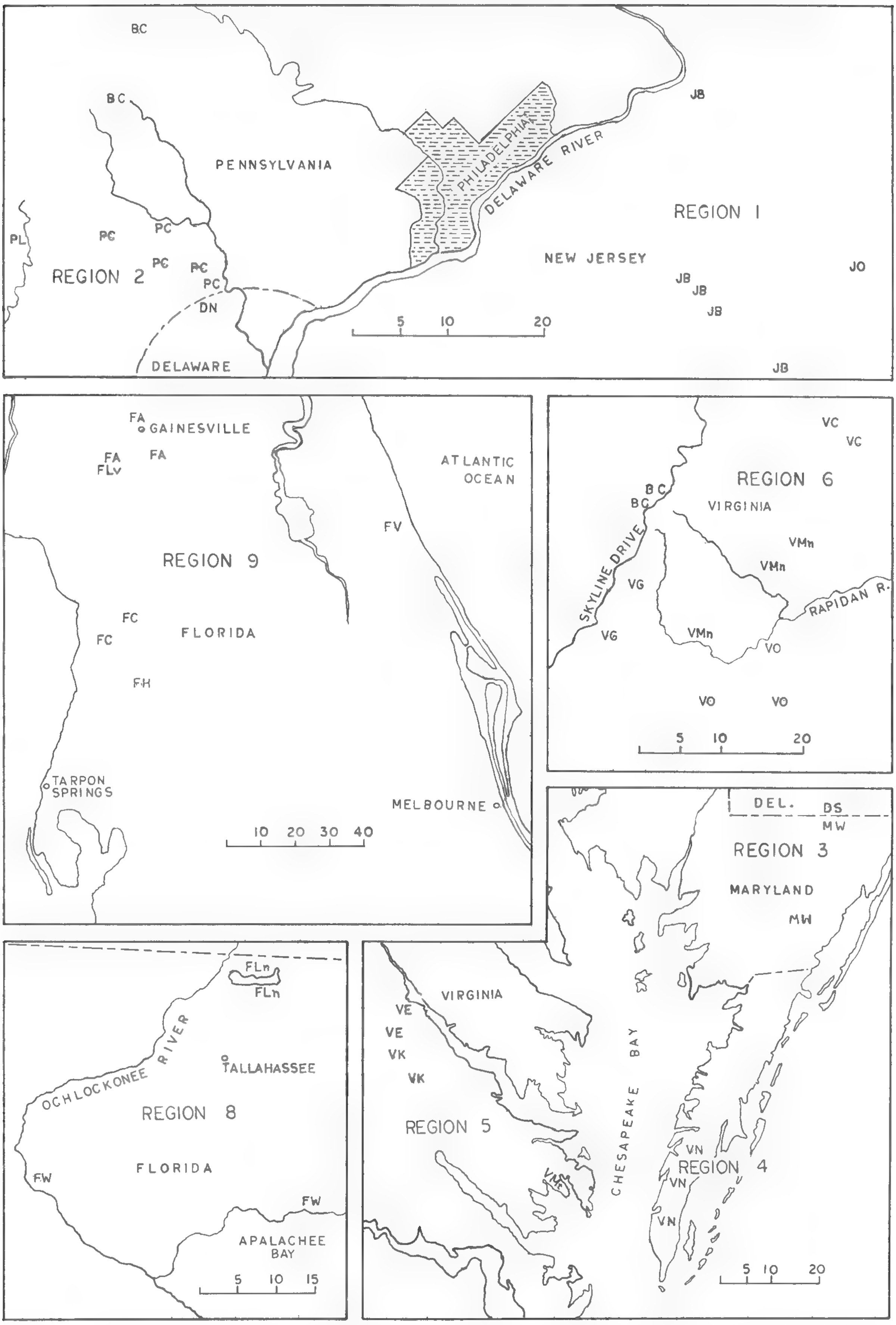
BC
BC
PENNSYLVANIA
PHILADELPHIA
DELAWARE RIVER
JB
REGION 1
NEW JERSEY
PL
PC
PC
REGION 2
PC
PC
PC
DN
DELAWARE
JB
JB
JB
JO
JB
5
10
20
FA
GAINESVILLE
FA
FA
FLv
ATLANTIC
OCEAN
FV
REGION 9
FC
FC
FLORIDA
FH
TARPON
SPRINGS
MELBOURNE
10
20
30
40
VC
VC
BC
BC
REGION 6
VIRGINIA
SKYLINE DRIVE
VMn
VMn
VG
VG
RAPIDAN R.
VMn
VO
VO
VO
5
10
20
DEL.
DS
MW
REGION 3
MARYLAND
MW
FLn
FLn
RIVER
TALLAHASSEE
OCHLOCKONEE
REGION 8
FLORIDA
FW
FW
APALACHEE
BAY
5
10
15
VIRGINIA
VE
VE
VK
VK
REGION 5
CHESAPEAKE
BAY
VN
REGION 4
VN
VN
5
10
20

Figure 1. Maps showing locations of eight of the nine regions where songs of the Carolina Chickadee were recorded. Region 7, covering the sea islands near Beaufort, South Carolina, is omitted. The letter symbols indicate the counties (see page 129) and show the recording locations. BC, in Regions 2 and 6, shows locations of recordings of Black-capped Chickadee songs.

Region 4	Northampton, Virginia	VN
Region 5	Essex, Virginia	VE
	King and Queen, Virginia	VK
	Matthews, Virginia	VMt
Region 6	Culpeper, Virginia	VC
	Greene, Virginia	VG
	Madison, Virginia	VMn
	Orange, Virginia	VO
Region 7	Beaufort, South Carolina	SB
Region 8	Leon, Florida	FLn
	Wakulla, Florida	FW
Region 9	Alachua, Florida	FA
	Citrus, Florida	FC
	Hernando, Florida	FH
	Levy, Florida	FL
	Volusia, Florida	FV

Lines 1, 2, 3, and 4 in Table 1 show the number of birds, the number of songs recorded, the number of birds represented by spectrographed songs, and the number of spectrographed songs from each region.

Parameters

Notes per Song. — I counted the number of notes in each recorded song from playback of the tapes at one-half, in some cases at one-quarter, normal tape speed. In a few instances I referred to a spectrogram to elucidate an unclear situation. Table 2 shows, by regions, the percentages of songs composed of different numbers of notes and the average number of notes for all songs. The most striking and significant fact here is the considerable divergence, in all but the first three regions, from the four-noted song which has been considered almost diagnostic (Brewer, 1961; Peterson, 1947; Pough, 1949; Saunders, 1951; Tanner, 1952).

Midpoint Frequency. — The majority of the notes of the Carolina Chickadee are maintained at close to a level frequency. We found, however, that the slurring of notes is common. When slurring occurs, it is typically initial and/or terminal in the note, and, although it may extend through a considerable range of frequencies, it is usually accomplished during a small part of the period of the note very rapidly—so rapidly that the human ear does not recognize it. When this type of slurring occurs, the rather level frequency of the middle section of the note usually determines the pitch—the frequency detected by the human ear.

As one basis for statistical comparison I measured the frequency of each note of the spectrographed songs at its midpoint without regard to any slurring. Table 1 and Figure 2 show the results for each region on a percentage basis.

The final histogram in Figure 2 shows the means of the regional frequencies of occurrence of the various midpoint frequencies. A dichotomy is obvious with well-developed concentrations about modes 3.5 and 6.4 kilocycles per second and a division at 4.7 kcs. Since the notes in each of these two

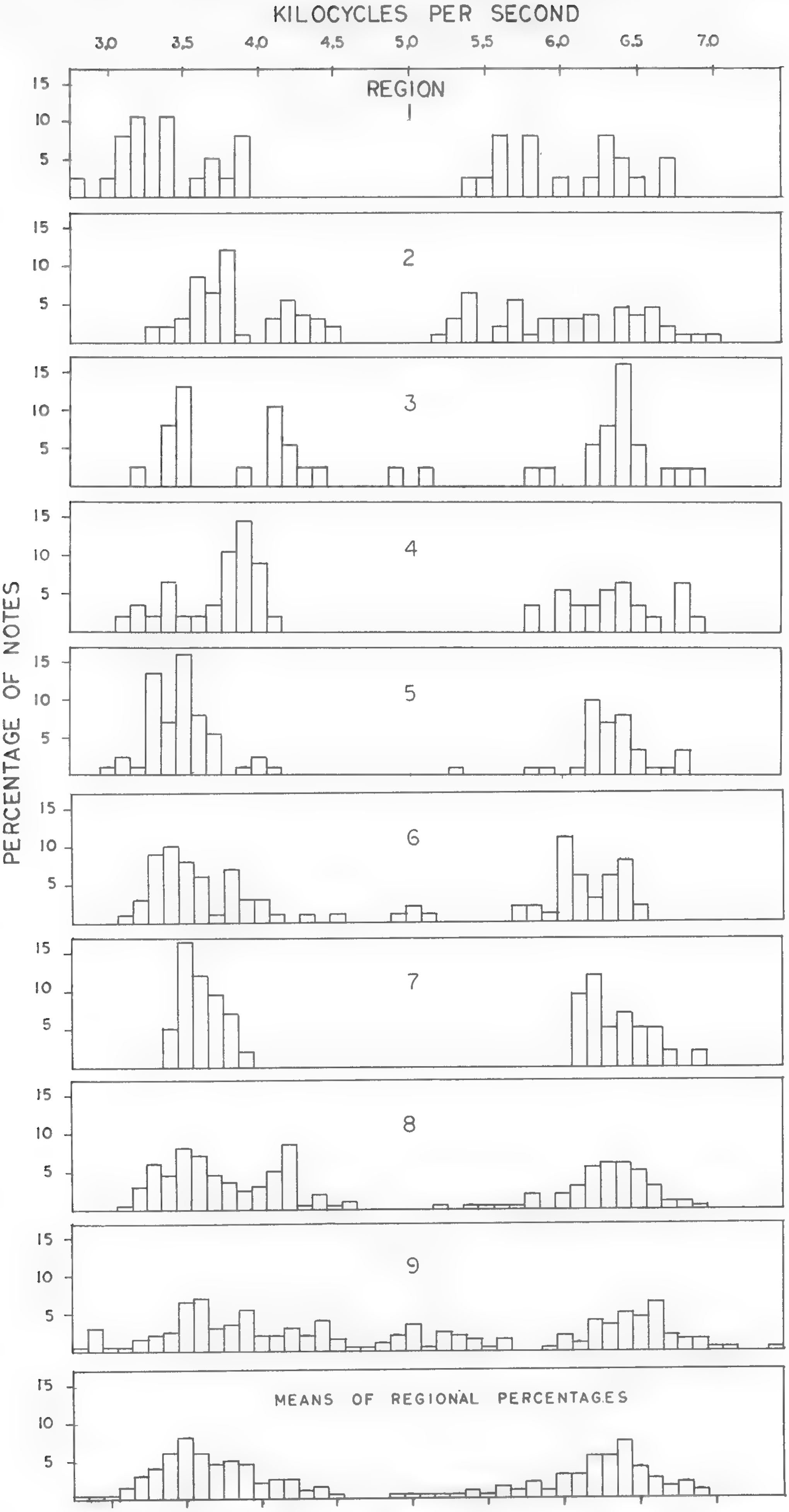

Figure 2. Regional distributions, by midpoint frequencies, of notes in songs of Carolina Chickadees expressed as percentages of all spectrographed notes from each region. Percentages are rounded to the nearest one-half. Relative relaxation of concentrations at modes is obvious in Region 9, particularly in contrast to the two clear modes and the division of notes into two ranges illustrated in the final histogram.

TABLE 1

Data on the Songs of the Carolina Chickadee Recorded in Nine Regions

Line number	*Region number*	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*Totals*
	Recordings										
1	Birds	9	17	9	21	12	17	6	16	23	130
2	Songs	129	444	116	318	218	310	121	361	689	2706
	Spectrograms										
3	Birds	8	13	5	14	10	13	5	12	19	99
4	Songs	9	26	9	16	17	24	11	30	65	207
	Midpoint frequencies in kcs.										
	High range										*Means*
5	Mode	5.60	6.40	6.35	6.20	6.35	6.20	6.30	6.35	6.40	6.24
6	Mean	6.05	6.05	6.24	6.35	6.36	6.05	6.35	6.27	6.08	6.20
7	S. D.	.41	.50	.48	.31	.33	.37	.22	.33	.66	.40
	Low range										
8	Mode	3.20	3.60	3.50	3.85	3.50	3.40	3.60	3.50	3.70	3.54
9	Mean	3.40	3.86	3.79	3.72	3.48	3.57	3.61	3.76	3.74	3.66
10	S. D.	.32	.32	.38	.27	.22	.29	.12	.37	.43	.30
11	Per cent of songs with regular pitch-alteration	89.1	99.5	100.0	51.3	49.1	30.0	95.0	33.2	88.2	70.6
12	Per cent of notes slurred	28.9	32.7	21.1	37.5	17.0	30.3	47.6	31.7	45.6	32.5
13	Mean variation in slurred notes in kcs.	.76	1.34	.56	.60	.60	.59	1.13	.90	.80	.81
14	Slur index	21.0	43.8	11.8	22.5	10.2	17.9	53.8	28.5	36.5	27.3

TABLE 2

Percentage Distribution of Carolina Chickadee Songs by Notes per Song

				Region Number					
Notes per song	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*
1		.5				1.0	.8		.4
2		.5		7.9		1.3			.1
3		2.0	.8	41.2	4.6	13.5	25.6	11.4	27.4
4	89.1	96.6	98.4	48.7	47.2	59.0	73.6	26.9	59.1
5		.2	.8	2.2	17.0	24.2		10.2	6.8
6	10.9	.2			12.8	1.0		50.4	6.0
7					4.1				
8								1.1	.1
9					9.6				
10					3.2				
12					1.4				
Average notes per song	4.22	3.96	4.00	3.45	5.23	4.07	3.74	5.04	3.91

groups tend to have some common characteristics distinct from those in the other, I find it convenient to identify all notes above 4.7 kcs as high range and all those below 4.7 kcs as low range.

Lines 5 through 10, Table 1, present the modes and the mean midpoint frequencies with standard deviations calculated for the means in both the high and low ranges. The mode is not the one most common frequency measurement, but rather is the median frequency of those five-consecutive-frequency measurements which include the largest number of notes. I consider this five-consecutive-measurement mode more truly indicative of concentrations than the usual single-measurement mode and used it also in analyzing the duration of the notes.

There are no significant differences in the modal or mean midpoint frequencies (Lines 5, 6, 8, 9, Table 1) except possibly in Region 1 and that is questionably significant because of the small sample. However, the extent of deviation from the respective mean frequencies (Lines 7, 10) varies considerably, particularly among the high-range notes in Regions 2 and 9 where the sample is larger and in Region 3, again a small sample.

Pitch-Alternation of Notes.—Orthographic representations of the typical Carolina Chickadee song all indicate, as in the *"fee-bee, fee-bay"* of Peterson (1947), a succession of higher-to-lower-to-higher-to-lower-pitched notes, which I call regular pitch-alternation. From playback of tapes and use of spectrograms I have inspected all songs containing a minimum of three notes and classified them as to the regularity of pitch-alternation. I made this count aurally and there may be a few inaccuracies, but, since pitch-alternation is almost without exception between notes in the high and low ranges, I believe the inaccuracies to be minimal. The results (Line 11, Table 1) show some rather extreme regional differences.

This inspection also showed that only 108 of the 2,706 songs started with notes in the low range. Of these, 24 were among the 318 from Region 4, and 45 among the 689 from Region 9. I found no songs among the 689 songs from Regions 1, 2, and 3 starting with notes in the low range.

Intra-Note Frequency Variation and Slur Occurrence. — Intra-note frequency variation, the difference between the highest and the lowest frequencies in one note, is used as the index of the extent of a slur. I measured this variation in the notes of all spectrographed songs.

In the field, we heard few notes of Carolina Chickadee song as slurred, yet the spectrograms show that slurring is common, particularly in high-range notes. The inability of our ears to recognize the slurs results from the rapidity with which they occur. For example, the first note of the song PC2-1, Figure 4, terminally descends from 6.2 to 3.8 kcs within about 0.04 second. These unrecognized slurs, which we believe are heard by us as a defect in the clarity of the note, may be the source of the "fricative or sibilant quality" mentioned by Saunders (1951).

We must consider song differences, however, as they sound to the bird. Generally accepted is the probability that birds have a shorter time perception smear and that they can resolve occurrences in sound of much shorter duration than can humans (Schwartzkopff, 1963: 106; Thorpe, 1961:4, 62, 125). These rapidly accomplished slurs may very possibly be identifying factors as important to a chickadee as are other elements more obvious to us.

Arbitrarily, I counted only notes containing intra-note frequency variations greater than 0.3 kcs as slurred. Line 12, Table 1, shows the percentages of all spectrographed notes which, on this basis, are slurred. Line 13 of the same table shows the mean intra-note frequency variation of the slurred notes as a group. A single slur index figure, the product of the mean regional intra-note frequency variation multiplied by the percentage of all slurred notes, appears in Line 14.

Note Lengths.—I have measured the duration of each note of the spectrographed songs. Figure 3 shows the regional results. Each bar indicates the percentage of all notes of each region found at each measurement, in gradations of 0.01 second. Also shown are the modal note lengths and the mean lengths with the standard deviations of the means.

The mean lengths are of course very much influenced by the quantity (e.g., in Region 8) or the relative absence (e.g., in Region 4) of short-duration notes. This largely determines the divergence of the mean from the mode. The five-consecutive-measurement mode for each region is shown in Figure 3 by a triangle on the base line. Figure 3 also shows the percentages of short notes — i.e., arbitrarily defined as notes lasting less than 0.11 second.

Perhaps significant are the differences in modal lengths which, in the first four regions, are from 0.28 to 0.26 second and elsewhere are 0.23 second or less. This difference may show a tendency for the more southern birds to sing shorter notes. If so, it is the only significant difference in song that appeared consistently over a wide range. While Region 4 (mode 0.28 second) and Region 5 (mode 0.19 second) are but 17 miles apart in direct line, the effective separation is closer to 200 miles because of Chesapeake Bay. The difference in note lengths does not correlate with the ranges of the accepted subspecies. In fact, I have found no correlation between song differences and subspecific differences.

The Recognized Influences on Song Variation

Although the existence of regional differences in the song of a single species of bird has long been recognized, the development of sound-recording apparatus has only lately given impetus to its scientific study. Thorpe (1961) and, to a greater extent, Armstrong (1963) reviewed the work done along this line. Of great importance to such studies is an understanding of the nature of the development in an individual bird of its own, more or less distinctive, mature song. Lanyon (1960) reviewed the work in this field. The following remarks are based largely on these three reviews to which I make specific reference only in the case of a quotation.

Territorial song (i.e., the advertising or primary song) of most passerine species develops from within inherited limitations typical of the species. An individual bird learns its definitive song over a period of time that varies with the species and may extend through the first spring. The forms of songs heard from other individuals of the same species strongly influence the form of its song which, after the learning period, is remarkably stereotyped and fixed for life.

Song, prevalent in one population, may vary from the typical, or from a form prevalent elsewhere, in one of two general directions: (1) toward increased stereotypy, or (2) toward relaxation of stereotypy. Again, a sterotyped form may be widespread and more or less typical for the species, or it may be a distinct and very localized form — a dialect.

At considerable risk of over-simplification, we may reduce the factors mentioned as influencing song variation to three: (1) local degree of population density, (2) association with a related and competitive species, and (3) existence or non-existence of a topographical or geographical barrier isolating one population from another.

Density of population promotes an increased stereotypy of song and at the same time enforces elements affording individual recognition. Sparsity of population encourages a loosening of stereotypy.

Association with a related and competitive species encourages the development of a stereotyped song along lines distinct from the song of the competitor. Such a development has some genetic basis as a reinforcement of the reproductive barriers (=isolating mechanisms of Sibley, 1961) between sympatric species where selection is against hybridization (Parkes, 1965).

The Carolina Chickadee has some association with one related and strongly competitive species, the Black-capped Chickadee, which is morphologically similar and seems to occupy an almost identical ecological niche. (The only other parid with which the Carolina Chickadee has contact in eastern United States is the Tufted Titmouse, *P. bicolor,* which is sympatric everywhere, morphologically distinct, and only slightly competitive.)

The Carolina and the Black-capped Chickadees are sympatric only in a few narrow zones of range overlap (Tanner, 1952; Brewer, 1963). In such localities hybridization is reported but selection seems to be strongly against it. Elsewhere, between the ranges of the two species, narrow, more or less unoccupied gaps seem to have developed as an isolating mechanism. However, where the ranges of the two chickadees meet and even along the gaps, song appears to be the major recognition factor, and difference in song is the only recognized behavioral or morphological isolating mechanism between the two sibling species.

Armstrong (1963:97) states: "In the absence of competition from related species, uniformity of utterance is reduced." Thus, where the Carolina and

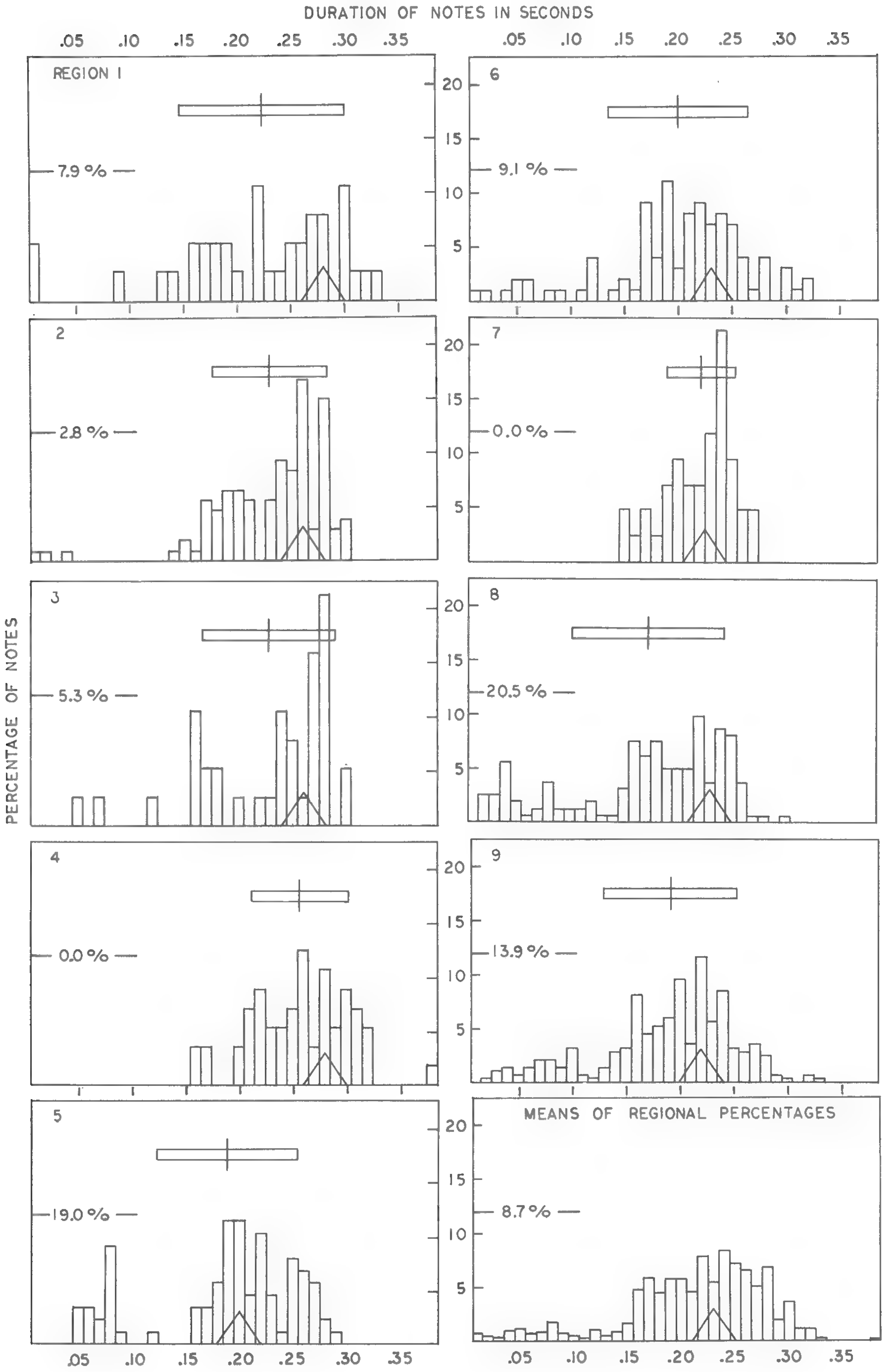

Figure 3. Regional distributions, by durations, of notes in songs of Carolina Chickadees expressed as percentages of all spectrographed notes from each region. The mean note duration for each region is shown by a vertical line, crossed by a rectangle which includes two standard deviations. Triangles on the base lines show the five-consecutive-measurement modes (see page 135). On the left of each chart are the percentages of notes lasting less than 0.11 second.

Black-capped Chickadees are allopatric, the influence of competition with a related and competitive species is weakened. Armstrong (1963:92) adds that "separation of one community from another is a prime factor in permitting divergence in song and generating dialect variations. Separation is probably always initially topographical or geographical." And in defining a dialect he wrote (1963:91): "There may be differences in the inflection of notes, in the quality and number of notes uttered or their order, in rhythm, length of phrase, the number and order of song versions, or other characteristics, though there must be a constancy of variations, or in the limits of variations in the community, for their utterances to constitute a dialect." According to Marler and Tamara (1964), "The term 'dialect' seems appropriate for the properties of the song patterns that characterize each separate population of breeding birds." Dialect, as I use it here, has possibly a narrower meaning in that it applies only to a song form that is distinct from the normal and prevalent in a limited area. In a dialect there must be a strong tendency toward a locally typical number of notes although some variation may occur. The order of succession of high- and low-range notes, of abnormally short notes, and of more typical length notes must be quite stereotyped. I would avoid, for example, recognizing an abnormal lack of stereotypy as a dialect when it is found as a localized phenomenon.

The Sedentariness of the Carolina Chickadee

The Carolina Chickadee is non-migratory and apparently so limited in movement that a single bird rarely travels more than a few miles from its birthplace. Dixon (1963), who studied a population on a 40-acre tract in Brazos County, Texas, for five years, found that, even in the fall and winter, adults restricted their activities to areas that were typically from 10 to 15 acres and seldom exceeded 20. These areas all included, or were near, their breeding territories.

In July 1962, I studied 115 recoveries (all that were available and reliable) of banded Carolina Chickadees from records of the Bird Banding Laboratory of the U. S. Fish and Wildlife Service. The location, given in these records, is within a "ten-minute block"—i.e., an area bounded by meridians and parallels of latitude and longitude at ten-minute intervals. One hundred and seven of the 115 recoveries were in the same ten-minute block as where the birds were banded; seven in laterally adjacent blocks; and one in a diagonally adjacent block. The maximum distance possible between banding and recovery in 107 cases is less than 15 miles and in any case less than 31.

A bias factor in the interpretation of this information is that birds tend to return seasonally to the same location — a breeding territory or feeding station. However, 30 of these records are free of this imputation because either the banding or recovery occurred in a period between 15 March and 15 May with a corresponding recovery or banding in a period between 1 September and 15 January.

According to general belief, normally sedentary birds do their greatest wandering in their first season immediately following emancipation from parental feeding. Unfortunately Dixon marked no birds between hatching and 7 October so that his work sheds no light on the dispersal of the birds in the first summer. The records of the Banding Laboratory and correspondence with banders of recovered birds, banded as nestlings or immatures, produced information on seven birds. One of these, banded as a nestling, was recovered seven and a half years later, 5.5 miles from the banding location. The remaining six were all recovered at or very close to the banding location, all more than 20 months after banding. This information implies that even birds of the year remain close to the parental territory.

The extremely sedentary behavior of the Carolina Chickadee may be an important factor in the degree to which the ontogeny of its song is the result of very localized influences.

Regions 1, 2, and 6

Of the nine regions, only Regions 1, 2, and 6 are close to the breeding-range limit shared by the Carolina and Black-capped Chickadees. The Black-capped apparently invades each of these regions in winter and birds of the two species mingle in small bands. I base my statement regarding the winter invasion of Black-capped Chickadees in Region 6 on hearing a Black-capped Chickadee song in Orange County on 22 March 1963.

The recording made farthest north in Region 1, JB1, is about 18 miles, almost certainly not over 30 miles, from the supposed southern limit of the breeding range of the Black-capped Chickadee in New Jersey. The most distant recording was made about 32 miles farther south.

We made some recordings in Region 2 within 13 miles of birds heard singing the typical Black-capped Chickadee song in the nesting season and additional recordings in an area that extended about 10 miles farther south.

In Region 6, which lies just southeast of the Blue Ridge in north-central Virginia, the proximity of the breeding ranges of the two birds is questionable. Tanner (1952), in his map of nesting-season records of the two species, indicates that, in this area, even the crest of the Blue Ridge is within the range of the Carolina Chickadee. He based this (pers. commun.) on collected specimens and information from Dr. Alexander Wetmore. However, I have reason to believe that there are some Black-capped Chickadees, or at least hybrids, nesting in the area.

On 16 May 1963, I recorded completely typical Black-capped Chickadee songs in the Big Meadows Swamp (elevation 3,500 feet) along the Skyline Drive. Although we broadcast pre-recorded calls of a Carolina Chickadee, we heard only Black-capped Chickadees at that time. Again on 18 and 19 May 1965, I recorded Black-capped Chickadee songs at Big Meadows, and also recorded three- and four-noted songs from the same bird. On 19 May 1965, I also recorded songs at Spitler Knoll Overlook (elevation 3,200 feet), 2.3 miles north of the Big Meadows Swamp. One of the 18 songs of the Spitler Knoll Overlook bird was three-noted; all the others were typical of the Black-capped Chickadee song which is two-noted. The songs with more than two notes all included notes within the high range (above 4.6 kcs) which I consider to be distinctive of the Carolina Chickadee song and outside the frequency range of the song of the Black-capped Chickadee.

On 18 May 1965, 0.9 mile from Big Meadows Swamp, I recorded songs of a third chickadee. These songs were four-noted only and, while not with regular pitch-alternation, they were quite similar to songs of other birds recorded well within the range of the Carolina Chickadee. On 20 May 1965, we recorded three- and four-noted songs with other Carolina Chickadee attributes, 4.5 miles north of Big Meadows Swamp at an elevation of 3,250 feet.

We found no evidence that birds giving the Black-capped Chickadee songs were breeding, except that their vocal and behavioral responses to our broadcast (i.e., of the calls of the Carolina Chickadee and the songs of both the Carolina and Black-capped Chickadees) gave every indication of territorial defense. In any event there were birds present in the breeding seasons of 1963 and 1965 which sang, predominantly, songs which, from the spectrograms, are (1) essentially indistinguishable from the songs of the Black-capped Chickadee recorded in the Pocono Mountains of Pennsylvania and in Massachusetts, and (2) completely distinct from any spectrographed songs of indisputable Carolina Chickadees.

Region 6 extends to within 6.5 miles of Big Meadows Swamp and Spitler Knoll Overlook, but it is lower in altitude by at least 2,500 feet and thus should be considered to be effectively at a greater distance (cf. Tanner, 1952).

It would seem that in Regions 1, 2, and 6 the population density, the absence of barriers to free movement, and some degree of association with the Black-capped Chickadee would exert similar influences on the prevailing song forms of Carolina Chickadees.

Tables 1 and 2 show a good degree of similarity between the song found in Regions 1 and 2 except for the intra-note frequency variation. One of the nine birds in Region 1 consistently inserted very short notes, identifiable from spectrograms and slow playback, preceding what would otherwise be the normal second and fourth notes. This was the only divergence from the notes-per-song and regular-pitch-alternation indices in the two regions.

There is a consistent difference between the intra-note frequency variation measurements, evidenced by the slur index figures of 21.96 and 43.82 in Table 1. The index for Region 2 is the highest of the nine regions. Inspection of the basic data shows that this is a reflection of a general tendency for notes in the high range to contain deep, rapidly accomplished down-slurs, so rapidly accomplished (e.g., PC2-1, DN1-5 in Figure 4) that they are not obvious in the field.

Song in Region 6 is very distinct from that found in Regions 1 and 2. All indices in the tables are radically different except in the midpoint frequencies. The high degree of stereotypy of song found in Regions 1 and 2, together with the similarity between the song forms of these two regions, may well be examples of the effects of the similar influences exerted by contact or proximity to the range of the Black-capped Chickadee and similarly dense populations.

Although proximity to the range of the Black-capped Chickadee in Region 6 is questionable (I have no authority but my own observation), the birds along the Blue Ridge were singing the Black-capped Chickadee territorial song and I did hear a song in the middle of Region 6 in March. The population of Carolina Chickadees was dense in most parts of Region 6, with suggestions of one or two lacunas. The song for Region 6 is, however, distinctly aberrant. Five- and six-noted songs were common; the percentage of regularly pitch-alternated songs is extremely low.

I cannot explain the difference between song in Regions 1 and 2 and Region 6 on the basis of the three general factors which have been mentioned as influences affecting the form of developed song.

Region 3

In 1963 and 1965, we collected a moderate sample in Region 3 in an area at and just below the southern border of Delaware, 100 miles south of Region 2. The population was dense and the birds never have contact with the Black-capped Chickadee. In important respects this sample shows the most strongly

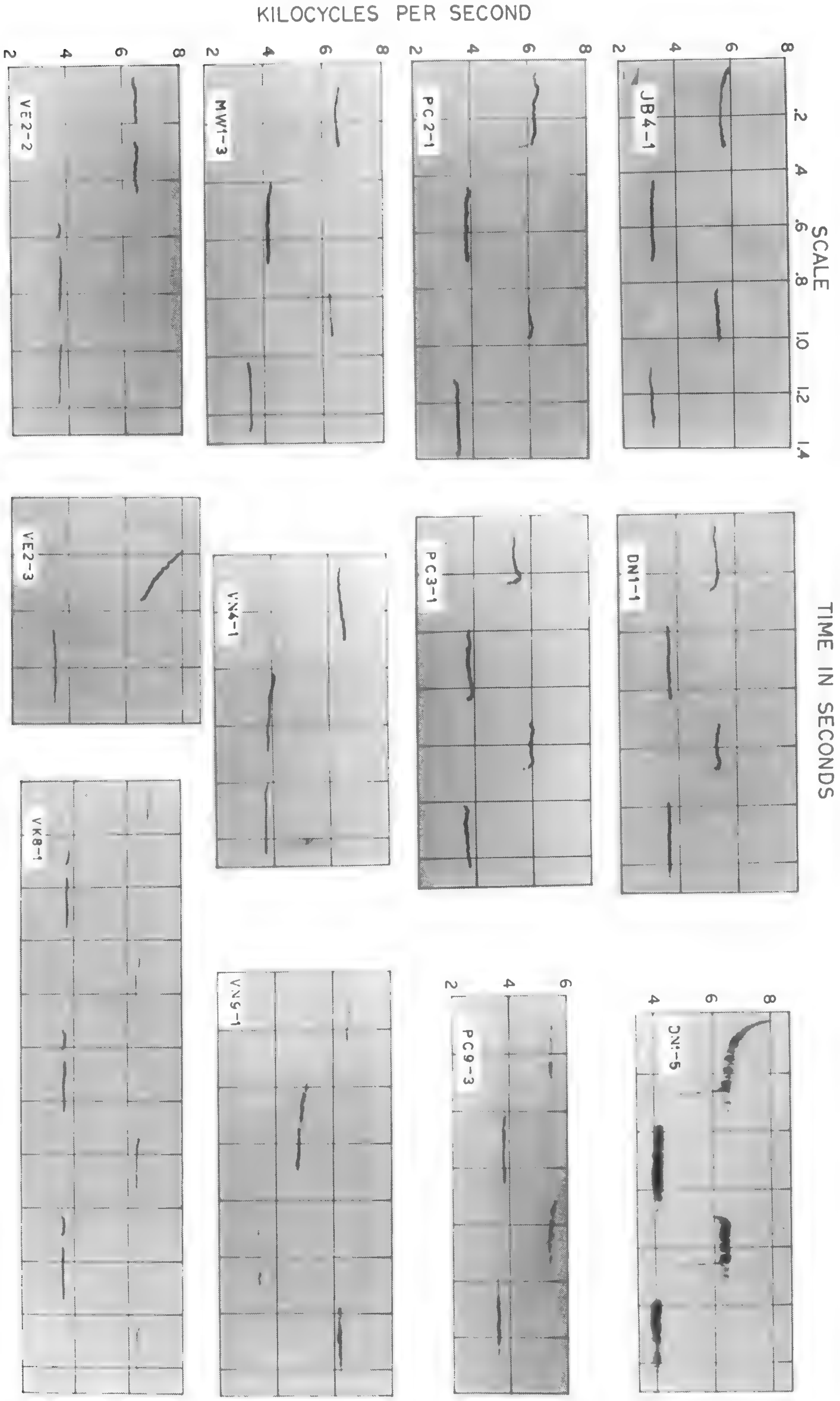

Figure 4. JB4-1, DN1-1, DN1-5, PC2-1, PC3-1, PC9-3, and MW1-3 depict normal songs of the Carolina Chickadee. DN1-5, reproduced at the wide band setting, and PC2-1 illustrate the deep and rapid down-slur somewhat typical of Region 2 song and not humanly audible. The first note of DN1-5 extends through an octave. DN1-5 and VE2-3 have the maximum frequency of all the songs, 8 kcs. VN4-1 is typical of the Region 4 dialect. VE2-2 and VE2-3 are two diverse patterns sung by one bird. These together with VK8-1, and VE1-1 and VK1-1 on Figure 5 show diverse songs found in Region 5.

developed degree of song stereotypy found. All but two of 116 songs were four-noted, and all were regularly pitch-alternated. Slurring was minimal. There are no abnormalities or extremes in the song from this region.

Regions 4 and 5

Regions 4 and 5 are separated by Chesapeake Bay, an effective barrier to any direct contact between the two resident populations. Topographically the two regions differ somewhat. One is low, flat, and sandy and the other somewhat rolling with a much heavier soil. Both are largely farmed but have frequent wooded areas. The populations were dense in appropriate habitats on both sides of the bay.

In Region 5, there is no apparent barrier to movement of chickadees or to contact with others to the north and west. In Region 4, on the other hand, movement and contact with others beyond the region is severely restricted. This region comprises the southernmost 24 miles of the Delmarva Peninsula down to Cape Charles. The maximum width of habitat for chickadees is eight miles, narrowing to four miles at the northern end. Here is a population of birds cut off to an unusual degree from flow of outside influence. Considering the sedentariness of the species, the effective extent of isolation, particularly of the birds in the southern end, probably approaches that of less sedentary birds on islands.

In Regions 4 and 5, the prevailing song is unusual and very distinct from the typical. And each is different from the other.

The peninsular birds, Region 4, have a well developed and formalized dialect consisting of one introductory note in the high range followed usually by two, sometimes only by one, and, in the case of one bird, by three relatively long notes of approximately equal pitch in the low range. With rapid slurs uncommon, they sound clear and musical to the ear. Of 21 birds in the region, seven sang this form exclusively and two more included it with more normal or with other abnormal forms. Of 318 songs recorded in two different years, 134 were in this dialect.

From a single bird in Region 6, I recorded a few songs that were rather similar yet have recognizably shorter notes and shorter intervals between the notes. This dialect song, even the two-noted form, is not in the least like the song of the Black-capped Chickadee. The frequency level of the first note is above 6 kcs. I have not found a first note of the Black-capped song above 4.1 kcs. The musical interval between high and low notes of the Black-capped's song is probably not more than two half-tones. The dialect song, in Region 4, had a typical interval of seven half-tones.

The average number of notes per song in Region 4 is the lowest we found. The mean note duration is the greatest, with a well developed modal concentration on 0.28 second, the same as in Region 1. The standard deviation from the mean length is unusually small.

Across Chesapeake Bay, in Region 5, the average number of notes per song is the greatest for any region; and the modal length of note, 0.20 second, is the shortest for any region.

Immediately noticeable in the song in Region 5 was an extraordinary variation when tested by such parameters as notes-per-song and pitch-alternation (VE1-1, VE2-2, VK1-1, and VK8-1 in Figures 4 and 5). The slur index is the lowest for any region, yet the slurs which we found were relatively slow and could be recognized. VE2-3 in Figure 4 was a most peculiar song.

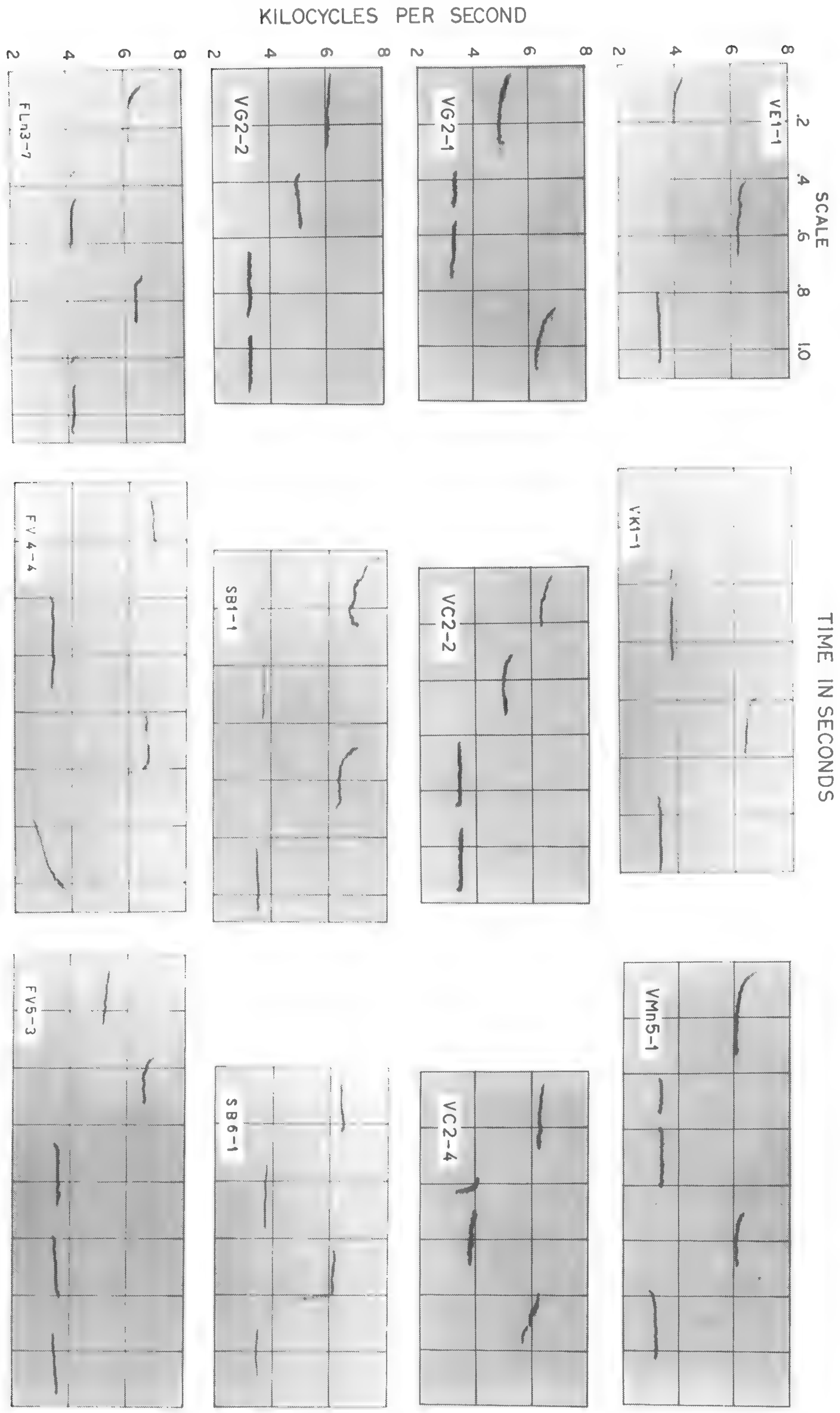

Figure 5. VG2-1 and VG2-2, and VC2-2 and VC2-4 are pairs of dissimilar patterns sung by two Carolina Chickadees. These, with VMn5-1, are from Region 6, where diversity of song is typical. SB1-1 and SB6-1, Region 7, are "normal" songs, but notice the terminal down-slurs similar to Region 2, in the latter. FLn3-7 is typical of the Iamonia dialect, Region 8. Compare it with VE2-2 and VK8-1, Figure 4. FV4-4 illustrates an abnormal and audible up-slur.

The development of a stereotyped dialect in Region 4 may be an indication of the influence exerted by the geographical isolation. I cannot explain so easily the peculiarities of song in Region 5. According to Armstrong, I should expect a barrier to association with others or a low population density.

Region 7

The sample collected (121 songs from six birds) in Region 7, which covers three sea islands off South Carolina, is probably small to serve as a basis for reliable generalizations. One of the six birds produced 29 songs that had only three notes. Twenty-four of these songs were particularly unusual in that the initial note was in the low range. In other words, they were typical songs beheaded by the elimination of the expected note in the high range. We noticed no other peculiarities except extensive slurring both in degree and in frequency of occurrence, quite similar to the slurring in Region 2. Some of this slurring was gradual, but the more typical was nearly vertical.

Regions 8 and 9

In Region 8, a relatively compact area in western Florida, we found 13 of the 16 birds within eight miles of the Georgia border and within a mile or two of Lake Iamonia; two in the St. Marks National Wildlife Refuge in Wakulla County; and one about 35 miles to the southwest near the Ochlockonee River. Region 9 has an extreme measurement of some 78 miles, from Gainesville to Brooksville in north-central peninsular Florida.

Measured by such parameters as notes-per-song, regular pitch-alternation, and mean length of notes, the song in Region 8 is decidedly abnormal. These aberrations derive from the existence of a stereotyped and dominant dialect found in the Iamonia section. The distinctive mark of this dialect is a doubling of each note in the low range. FLn3-7, Figure 5, shows the typical form of an Iamonia dialect song. The first note of such a pair is always of short duration, usually from 0.02 to 0.05 second, and is at the same, or approximately the same, frequency as the second. Figure 3 illustrates how often we found these short notes in Region 8. The first impression in the field is of one continuous note containing a short modulation of sound, and suggesting the "slight waver in the middle . . . *fee-beyee*" that Saunders (1946) found sometimes in the second note of the Black-capped song. However, sound spectrograms show there is actually an interval of silence. Spectrograms of the variant of the Black-capped song show that the "waver" is close to the midpoint of the note and that there is apparently not a silence but merely a short and relatively sharp reduction in sound volume.

In some of these dialect songs, paired notes appear only as the second and third in a song, the final note being single.

Twelve of the 13 birds recorded in the Lake Iamonia area produced a song in this dialect. Of 316 songs recorded there, 214 contained one or more of these paired notes. We recorded songs with similar characteristics from a few birds in Region 5 (VE2-2, VK1-1, and VK8-1 in Figures 4 and 5) but did not find it anywhere else in Florida.

The population density in the Iamonia area was heavy. We did not ascertain the limits of the area in which this dialect prevails, but we heard a few non-dialect songs about 12 miles south and neither the birds at the St. Marks Refuge nor the bird at the Ochlockonee River sang it. In Region 8, there is no apparent topographical or geographical barrier to free movement from the region. The ecology seemed favorable in all directions.

In peninsular Florida (Region 9) the situation with respect to population density is different. Correspondence with ornithologists and local bird club officials produced the following comments: Ormond Beach, "occasionally—but not usually—see them on our Field Trips"; DeLand, "very rare in this area"; Maitland, "believe I have not seen a Chickadee [since 1947] in this section"; Brooksville, "they are here, not in too great numbers." Near Gainesville we searched and broadcast the song in three or four suggested locations for one entire day before we found any birds. Sprunt (1954) says, "South of a line from Tarpon Springs (west coast) to Melbourne (east coast) the chickadee is a definitely uncommon to nonexistent bird." We made recordings within about 27 miles of this line.

Keeping in mind the sparsity of the population in Region 9, one could look for the result of the influence referred to by Armstrong (1963:64), "Where birds breed near the limits of their geographical range or climatic tolerance the sparseness of individuals and reduction in vocal competition would tend toward the relaxation of rigidity of song structure."

In Region 9, less than 60 per cent of the songs are four-noted, which is below the average but not extreme. Statistically the most striking aberration is in the failure of concentration of the midpoint frequencies of notes at modes, apparent in Figure 2. The standard deviations from mean frequencies in both the high- and low-range notes (Lines 7 and 10, Table 1) are the highest. The percentage of notes slurred is relatively high but the slurs are not deep (intra-note frequency variation). The result is a slur index figure only a little above the average.

An impression of diversity in song forms (more important than is apparent from the application of the parameters) was gained in the field in Region 9. The spectrograms show that the peculiarities are to a considerable extent in what might be called the shapes of the notes — i.e., the shapes of the spectrographic traces. We found gradual slurs, therefore audibly comprehensible, more often in Region 9 than elsewhere. A remarkable number were in the unusual upward direction (FA2-1 and FV4-4 in Figures 5 and 6). Variation in the song forms occurred in the successive songs of a single bird to an unsual extent.

FC2-5 in Figure 6 is reproduced at one-half normal tape speed and at the wide band setting of the spectrograph to illustrate better the very odd first note. Additional analysis of this note, made by Mr. C. H. Greenewalt with his ultra-sophisticated oscillograph, confirms that it is an example of "two voices" — i.e., of two distinct sounds made simultaneously and independently of each other by one bird. FC2 sang other notes of this type, but I have not found clear examples of the two-voice phenomenon from other chickadees.

Generalizations as to Regional Song

There is a persistent appearance over its entire range in the eastern United States of what is generally accepted as the normal or typical song of the Carolina Chickadee. I describe this as consisting of four whistled notes, of which the first and third are pitched at frequencies from 6 to about 6.8 kcs and the second and fourth between 3 and 4.2 kcs; the notes are of approximately equal duration, usually from 0.15 to 0.28 second, with a rhythm but slightly if at all accented, and without humanly noticeable slurring.

The normal song was found very consistently in central New Jersey, in southeastern Pennsylvania and northern Delaware, in Maryland just south

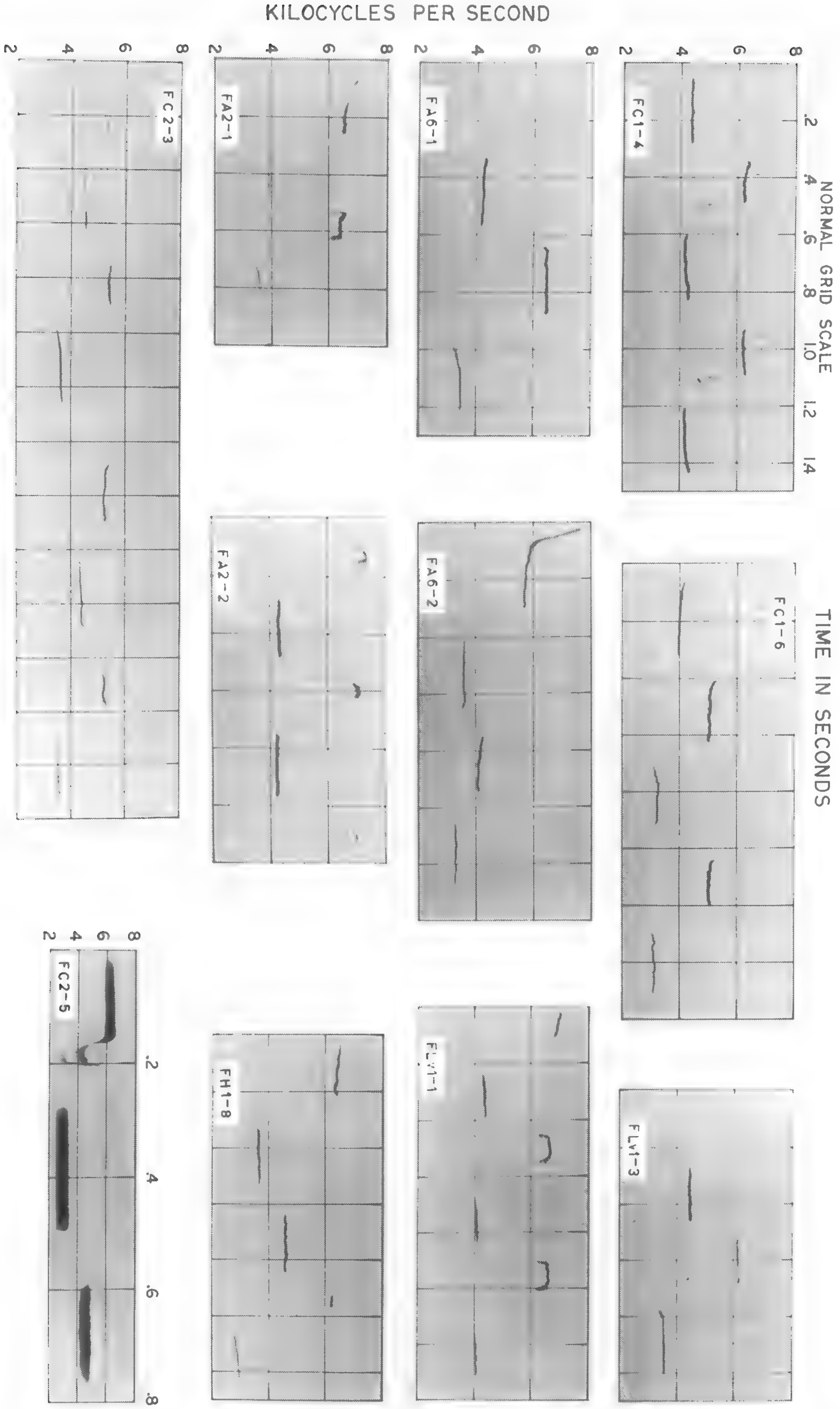

Figure 6. Five pairs of Carolina Chickadee songs, each pair from one bird, show the variation in "note shapes" particularly found in Region 9. FC2-3 is an example of an extension of a fairly normal song without variation of the pattern. The first note of FC2-5, reproduced at one-half speed and at the wide band setting, is the only example found of two-voice song. These, with FV4-4 and FV5-3 on Figure 5, are all from Region 9.

of the Delaware border, and near Beaufort, South Carolina. In the five remaining regions about one-half to less than one-fourth of the recorded songs conform to this standard.

There is a definite tendency for a Carolina Chickadee within any one region to sing in a manner consistent with the song of others in the same region. The regional manner of singing may focus on the accepted typical song form of the species, may be typified by a stereotyped but distinct dialect form, or may have fluidity as its common denominator — i.e., a consistent freedom from any stereotypy.

One may recognize atypical songs in the field by one or more of certain factors: (1) variation in the number of notes, (2) frequent abandonment of regular pitch-alternation, (3) initial notes pitched lower than second notes, and (4) the frequent appearance of audible slurs. In the spectrograms, other differences appear.

In Regions 1, 2, 3, and 4, the modal length of notes are from 0.26 to 0.28 second; and elsewhere these modes are from 0.20 to 0.23 second.

The pitch of notes, as exemplified by the regional midpoint frequencies, is rather consistent everywhere. The midpoint frequency modes vary little in the nine regions except for appreciably lower modes in the songs from New Jersey birds. However, there is a diversity in the degree of concentration at or near these modes. Whether measured by the percentage of notes falling outside the 6–6.8 and 3.1–4.2 kcs ranges or by the degree of concentration within any five-consecutive-frequency measurements, the concentration is weakest in Regions 1, 2, and 9 and strongest in Regions 5 and 7. These percentages are summarized below.

Regions	*Percentage within any five-consecutive-frequency measurement*	*Percentage outside 6-6.8 and 3.1-4.2 kcs range*	*Song pattern*	*Proximity to Black-capped Chickadee*
1	52.5	26	strong	close
2	48	32.5	strong	close
9	49	30	weak	none
5	79.5	4	weak	none
7	88.5	2	strong	none

The above summary shows that the concentration within any five-consecutive-frequency measurements is high in Regions 5 and 7 and low in Regions 1, 2, and 9. The percentage of notes falling outside the 6–6.8 and 3.1–4.2 kcs ranges is very low in Regions 5 and 7 and high in Regions 1, 2, and 9. There is no correlation between either midpoint frequencies or stereotypy of song patterns on the one hand and either population density (lowest in Region 9) or proximity to the range of the Black-capped Chickadee on the other.

The amount of slurring of notes, everywhere more common and extensive among notes in the high range than in the low, varies and seems to show some regional correlation. Deep slurs — i.e., slurs extending through a wide range of frequencies, as tested by the percentage of notes with intra-note variations greater than 1 kcs — were found much more commonly in Regions 2 (21 per cent) and 7 (19 per cent). Elsewhere the highest such percentages were 11 and 5. There is not a wide variation from region to region in the occurrence of more shallow slurs whose frequency varies from 0.3 through 1 kcs. The amount or the extent of slurring seems to have no correlation with population density, normality of song pattern, or proximity to a competitive species.

Generalizations as to the Individual's Song

My number of spectrograms is hardly sufficient to provide reliable data with respect to the songs of an individual bird, so that any conclusions must rest mainly upon the elements we can recognize audibly, such as notes-per-song and patterns of succession of notes in the two ranges, with some recognition of audible slurring and of very short notes.

We found some tendency everywhere for a bird to change the form of its common song by dropping or by adding one or more notes at the end without changing the basic pattern. (*Pattern* here refers to the order of succession of high- and low-range notes and of very short notes. For example, HLHL expresses the typical song of four notes successively in the high, the low, the high, and the low frequency ranges. HLHL changed to HLH or HLHLHL means a change only in the form of the song; HLHL changed to HLLH represents a change in the pattern of the song.) In the songs of individual birds, changes in form appear more often than do changes in pattern.

Obviously there is little variation among the songs of a single bird in Regions 1, 2, 3, or 7 since there is little variation from the normal in these regions. The six-noted songs in Region 1 were from a single bird and formed its entire repertoire. Of the 31 six-noted songs in Region 7, 29 were the only songs recorded from a single bird.

On Cape Charles, Region 4, the birds to a large extent sang either the normal song or the dialect, but some fluidity in the song of the individual was obvious. In most cases this was a change in form without departure from the basic pattern. Eleven of the 21 birds changed the number of notes while singing.

Across Chesapeake Bay, in Region 5, this tendency was even more obvious. Seven of the 12 birds sang with differing numbers of notes. Here also each bird tended to have its own pattern. VK8, for example, had songs with six, seven, nine, and twelve notes, all following the scheme of HLLHLL. There were pattern changes in some cases. VMt1 sang HLHL, HLLH, HLLHL, and HLLHLL. VE2's songs, written HLHL, HLH, HHL, and HHLL, included the most unusual form of slur (VE2-3 in Figure 4).

In Region 6, piedmont Virginia, we found that 10 of the 17 birds varied their songs with still greater freedom. Seven sang more than one pattern.

In the Florida panhandle, Region 8, seven of the 16 birds varied their songs but the patterns were practically limited to two, the normal and the Iamonia dialect with its doubled note in the low range. Four of the 16 birds sang both the normal and the dialect patterns.

Among the peninsular Florida birds, Region 9, freedom from restriction of any bird to one song form is most obvious. Sixteen of the 23 birds varied their songs. One sang eight different songs in four distinct patterns. Six had three patterns to their songs and five used two patterns.

Rationale of the Variations

Except for Regions 4 and 9 it is difficult to relate the special characteristics of song found in the nine regions with the bases advanced in Armstrong's review (1963) as influential in reducing, promoting, and directing song variation. Region 4 has a partial, but probably very effective, geographical barrier to free movement and to association with others of the species. We found a stereotyped dialect here as should be expected. In Region 9, where the density of the population is low, the relaxation of stereotypy is obvious and to be expected.

However, it seems impossible to justify the peculiarities found in Regions 5, 6, and 8 on any of the proposed bases. In Region 8, we found the strongest example of a highly stereotyped, strongly predominant, distinctive dialect, with no isolating barriers present. Song in Regions 5 and 6 was almost as, if not as, free from stereotypy as in Region 9 on the Florida peninsula, notwithstanding high population density, absence of barriers to movement, and, in the case of Region 6, proximity to birds singing the song of the competitive sibling species, the Black-capped Chickadee.

Other important influences must work to promote the occurrence of localized variation in song. One element in the behavior of the Carolina Chickadee, which has not been, I believe, discussed, may be an effective isolating factor. This is its apparent immobility, its sedentariness throughout the year. The extent of the wandering of a young male bird during the period within which his definitive song is developing would determine the number of different birds whose song he hears. If, as it appears, even the Carolinas of the year move only in a small area, the songs the bird hears are limited to those which were learned in the same area. There would be a strong tendency favoring the development and fixation of one type of song in one relatively small population. One might conceive of a set of fortuitous circumstances—e.g., an unusual survival success among the descendents of a bird with an aberrant song—which would initiate the development of the local song type. In the absence of physical barriers, there would be edges of other influences, but in the heartland there would be a continuing reinforcement of the local song type.

If sedentariness could explain the existence of a dialect form such as we found around Lake Iamonia in Florida, it also could explain a local tendency toward variability. What we then need is a prototype of varied song rather than a stereotyped song.

Summary

During the nesting seasons of 1963, 1964, and 1965, my wife and I recorded on tape 2,706 songs of 130 Carolina Chickadees (*Parus carolinensis*) distributed among nine restricted regions from the northern to the southern limits of the range of this species along the Atlantic seaboard. By applying selected parameters to information obtained from sound spectrograms of 227 songs of 118 birds and from playback of the tape recordings, certain regional characteristics of song developed. Norms for the entire area were determined as the averages of the various regional characteristics.

Characteristics diverging considerably from the norms and from the traditional normal song of the species were found in five of the nine regions, and attempts to relate them to ecological, topographical, and geographical factors previously recognized as influencing song variation were rather unsuccessful.

The degree of sedentariness of a species is suggested as being influential in promoting or reducing the occurrence of localized song characteristics.

Acknowledgments

In finding the Carolina Chickadee, my wife and I had the assistance of many people, some in correspondence, some in conversation, and some in the field. Without naming them, I wish to express my gratitude, particularly to each one whose hospitality we enjoyed. I want to thank Dr. Allen J. Duvall, who made available the records of the Bird Banding

Laboratory of the U. S. Fish and Wildlife Service, and Mr. John V. Dennis, Mrs. James C. Robinson, and Dr. William P. Wharton, cooperators with the Service. I am indebted also to Mr. Crawford H. Greenewalt not only for making available his Sona-Graph but also for his very valuable comments and suggestions particularly in the field of acoustics. The Laboratory of Ornithology of Cornell University, originally responsible for my interest in recording bird song, provided the recording equipment. Among the staff of the Laboratory, I want to mention Dr. Peter Paul Kellogg who has been of invaluable help.

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SOME OBSERVATIONS ON HABITATS OF THE SWAINSON'S WARBLER

BROOKE MEANLEY

The Swainson's Warbler (*Limnothlypis swainsonii*) breeds locally in southeastern United States on the South Atlantic and Gulf Coastal Plains, in the southern Appalachians northward into West Virginia, and occasionally on the southern Piedmont Plateau (see Figure 1). Sprunt and Denton (*in* Griscom and Sprunt, 1957:50) generally characterize the breeding habitat for the greater portion of the population in the southeastern states as those swamps of the rivers that are subject to periodic flooding and "composed of fairly large trees with a dense under-story of cane, briars, vines, scrub palmetto, herbaceous plants, and young trees of the next succession." Other authors, who have given similarly general characterizations of the breeding habitat, are Brewster (1885), Wayne (1910), Brooks and Legg (1942), Sims and DeGarmo (1948), and Parnell and Quay (1964).

The purpose of this paper is to evaluate more exactly the features of the habitat that the Swainson's Warbler has selected on the Coastal Plain of Georgia and South Carolina and has been known to occupy longer than any other. In the course of the paper I shall compare the habitat on the Coastal Plain with the mountain habitat of the Swainson's Warbler on the Allegheny Plateau in West Virginia.

I first made observations on Swainson's Warblers in the upper Coastal Plain just below the Fall Line at Macon, Georgia, in the spring and summer of 1944 (Meanley, 1945), and additional observations in the same area during 1945-1946 and 1963-1965. I made other observations during 1960-1964 within a radius of about 50 miles of both Charleston, South Carolina, and Savannah, Georgia, and during May and June of 1965 I investigated the mountain habitat near Charleston, Kanawha County, West Virginia.

Present Status of Swainson's Warbler in Georgia and South Carolina

In Georgia and South Carolina, most of the Swainson's Warblers occur on the river floodplain forests of the upper Coastal Plain where one finds the most extensive growth of canebrakes (*Arundinaria gigantea*). Thus there appears to be a correlation between the breeding density of Swainson's Warblers and the distribution and extent of canebrakes. In this optimum habitat, Swainson's Warblers usually exist in small groups, such as are characteristic of Kirtland's Warblers (*Dendroica kirtlandii*) on their breeding ground in Michigan (Mayfield, 1960:52). Hence it is sometimes possible for a person to hear three or four male Swainson's Warblers singing at one time.

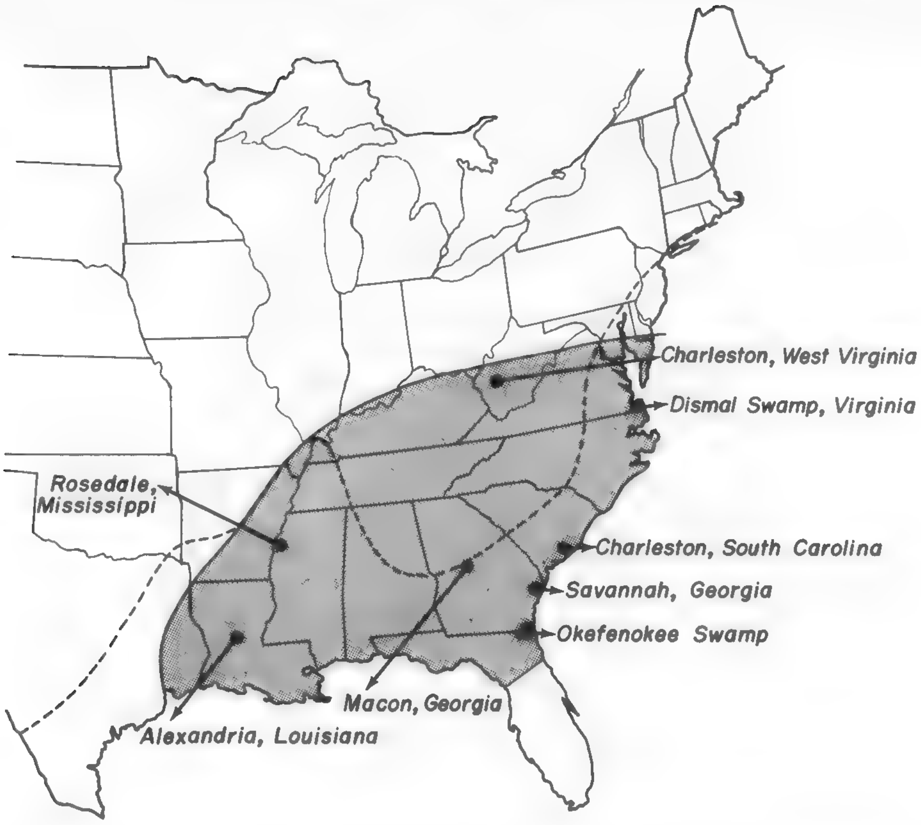


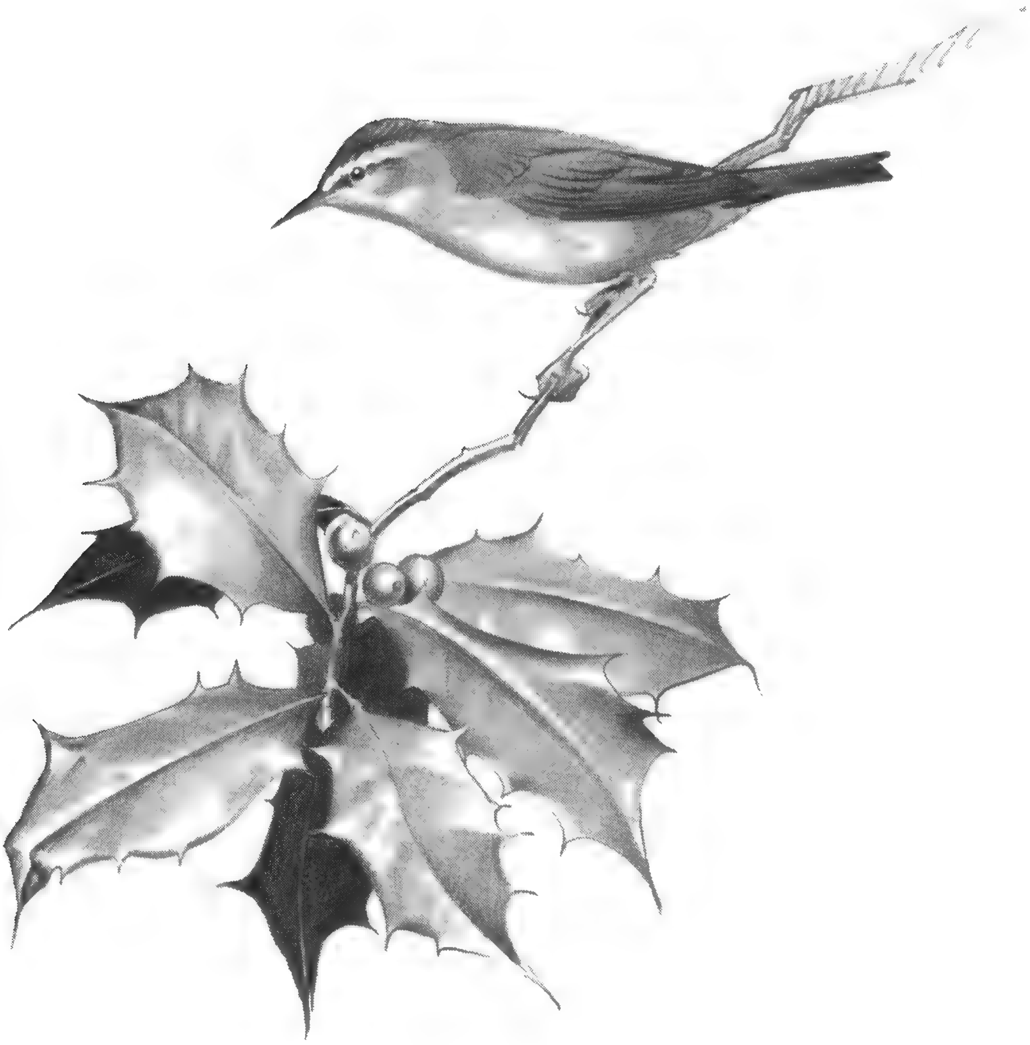
Figure 1. Map of eastern United States showing the approximate breeding range of Swainson's Warbler (shaded area), the estimated inland boundary of the Coastal Plain (broken line), and certain places mentioned in the text.

At the close of the 19th century and the beginning of the 20th, Swainson's Warblers were apparently more numerous in the lower Coastal Plain than they are today. Wayne (1910:149-150) found them to be common breeding birds near Charleston, South Carolina, as did Perry (1887:142) near Savannah, Georgia. During the period of 22 April to 25 September 1884, Wayne collected 47 specimens of this species near Charleston. Considering modes of travel available to Wayne and the limited area of his operations, his collecting of so many specimens would seem to indicate a sizable population in the area. Perry (1887) reported 24 active nests near Savannah in the spring of 1887, which likewise suggests that Swainson's Warblers were more abundant in the late 19th century than at present. E. S. Dingle of Huger, South Carolina, who worked with Wayne and who bridged the gap between Wayne's time and the present, informed me in April 1958 that he had noted during his lifetime a marked downward trend of the population in the coastal area. A. Sprunt, Jr. (*in* Sprunt and Chamberlain, 1949:435), a protégé of Wayne's, has seen this warbler only four times in the lower Coastal Plain of South Carolina.

In the lower Savannah River Valley, an area extending 30 miles upriver from Savannah, E. O. Mellinger and I found only scattered individuals and occasional pairs during the early 1960's — certainly not the numbers and concentrations found farther up the Valley near Augusta, as reported by Murphey (1937:42), Norris (1963:47), and J. F. Denton (pers. commun.).

Methods of Observation

I analyzed the vegetation in territories of the Swainson's Warbler by selecting one-fourth-acre plots or quadrats within the territories. My analyses of territories in canebrake were made during May 1963, approximately 5 miles south of Macon, and in scrub palmetto (*Sabal minor*) during May 1964, some 10 miles north of Savannah, Georgia, in Jasper County, South Carolina.



Swainson's Warbler. Drawing by Louis Darling, courtesy Houghton Mifflin Company.

For each stratum of the forest in the territories, I estimated the species composition and height of trees and shrubs. I recorded the diameter of trees and saplings at breast height (dbh). In the following text the strata are identified as follows: (a) upper canopy — largest and tallest trees, with dbh more than one foot; (b) lower canopy — smaller trees and saplings, with dbh under one foot, and tending to form a middle layer of the forest strata; (c) undergrowth — the canebrake of the upper Coastal Plain, and the scrub palmetto of the lower Coastal Plain; and (d) ground cover — low growing herbaceous vegetation, usually under two feet in height.

I determined the light-shading effect of the leaves in the Coastal Plain habitats and the density of the light in the feeding areas in both the canebrake and mountain habitats between 11:30 AM and 12:30 PM on windless days when the sun was shining. To estimate the light-shading of the leaves, I used a hoop, two feet in diameter and divided into eight sections. By holding the hoop directly overhead and sighting upward I made 20 readings, all at random, in the one-fourth-acre plots. To measure the intensity of the light, I placed a mirror on the ground in the exact spot where a Swainson's Warbler had been feeding less than one minute before, held a Weston Master IV exposure meter, with the photo-electric cell upward, one foot above the mirror, and took a reading.

I used territory-mapping and transect methods in making the censuses of the birds.

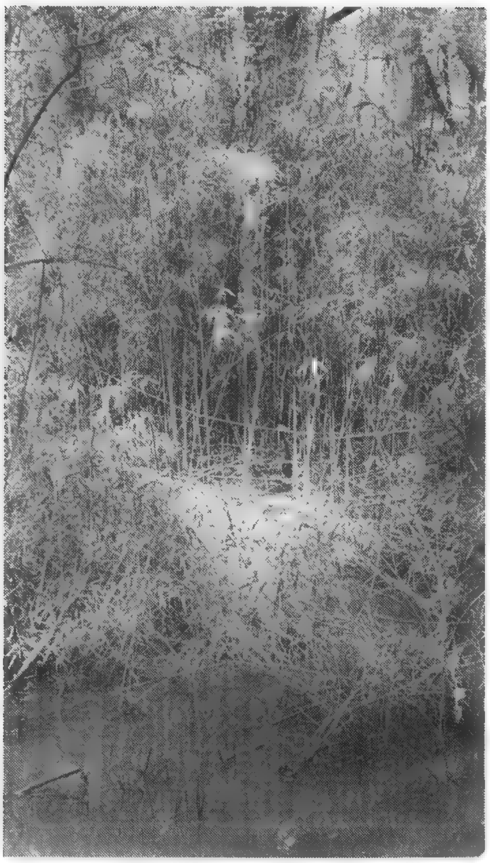


Figure 2. Canebrake habitat of Swainson's Warbler in Ocmulgee River floodplain forest near Macon, Georgia, April 1965.

Floodplain Forest-Canebrake Habitat

The floodplain forest bordering the Ocmulgee River south of Macon is part of a bottomland complex which, in this area, also includes extensive swamps of tupelo gum (*Nyssa aquatica*) and smaller swamps of shrubs (mainly of *Acer-Alnus-Viburnum-Vaccinium*). The floodplain forest bordering the river is flooded only for relatively short periods each year; the tupelo gum swamps, except in periods of extended droughts, always have some water present.

Cane grows extensively in parts of the floodplain forest (Figure 2). In some sections, canebrakes, in nearly pure stands, cover square-mile areas. Where the stands of cane are thin or where there are openings in the canebrakes and the light is more intense at ground level, herbaceous vegetation or briars (*Rubus* sp.) sometimes occur.

Canebrakes are the best habitat for Swainson's Warblers in the Macon area. Fifty-nine of the 62 territorial males that I observed in six breeding seasons had their territories in patches of cane growing beneath the floodplain forest canopy. The other three males were in drier parts of the shrub swamps along the upland edge of the bottomland.

Description of Sample Area. — See Table 1 for plant composition. The trees comprising the upper canopy of the forest were mainly hackberry (*Celtis laevigata*), swamp chestnut oak (*Quercus michauxii*), and elm (*Ulmus americana*). They averaged approximately 60 feet in height and 1.5 feet in diameter at breast level.

The smaller trees and saplings, mainly hackberry, ash-leaved maple (*Acer negundo*), ash (*Fraxinus* sp.), mulberry (*Morus* sp.), and swamp chestnut oak averaged about 25 feet in height.

Beneath this lower canopy grew the cane averaging approximately 15 feet in height and from one-half to one inch in diameter at ground level (Figure 3). The number of cane poles in 10 quadrats varied from 18 to 75 per 10-foot-square quadrat. There were about 20,000 cane poles per acre in my sample area which was virtually devoid of other plants, except for a scattering of large trees. The density of the combined upper and lower canopies and the cane undergrowth was about 85 per cent. In the interior, even herbaceous vegetation was absent, presumably because of the shading effect of the upper and lower canopies. Twelve exposure meter readings, made at feeding sites of the Swainson's Warbler in the canebrakes, ranged from 35 to 125 with an average of 77. The ground at the feeding sites was dry throughout the year except during periods of floods.

TABLE 1

Forest Composition in Two Swainson's Warbler Areas

Coastal plain	*Upper canopy Trees*	*Per cent*	*Lower canopy Saplings*	*Per cent*	*Undergrowth*	*Per cent*
Upper	Hackberry	38	Hackberry	44	Canebrake	100
	Elm	24	Boxelder	20		
	Swamp chestnut oak	24	Ash	12		
	Boxelder	14	Mulberry	12		
			Swamp chestnut oak	12		
Lower	Laurel oak	17	Sweet gum	27	Scrub palmetto	100
	Sweet gum	17	Red maple	18		
	Red maple	17	American holly	10		
	Elm	17	Laurel oak	9		
	Ash	12	Hackberry	9		
	Hackberry	10	Water oak	8		
	Water oak	10	Myrtle	8		
			Elm	5		
			Red bay	2		
			Loblolly pine	2		
			Swamp chestnut oak	2		
			Southern magnolia	2		
			Ash	2		

Swamp Forest-Scrub Palmetto Habitat

The territory of a male Swainson's Warbler, in Monkey John Swamp, approximately 10 miles north of Savannah, Georgia, was within a narrow band of scrub palmetto that lay between an inundated section of the swamp (Figure 4) and the upland. Bald cypress (*Taxodium distichum*) was the dominant tree species in the flooded section and there was virtually no undergrowth beneath it. The upland side of the palmetto strip, the drier side, was forested with a sweet gum-water oak *(Liquidamber styraciflua-Quercus nigra)* association and, in places, an undergrowth of mixed shrubs and briars formed dense thickets, apparently unsuited to Swainson's Warblers.

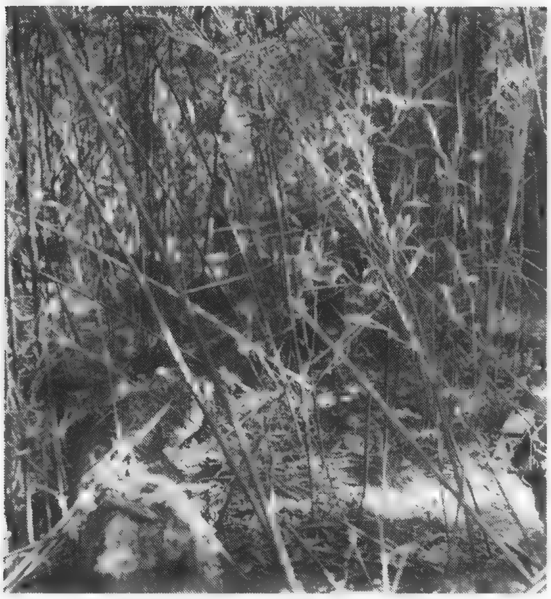


Figure 3. Part of canebrake territory of Swainson's Warbler in Ocmulgee River floodplain forest near Macon, Georgia.

Description of Sample Area. — See Table 1 for plant composition. The upper canopy of the forest above the scrub palmetto averaged about 75 feet in height and was composed of laurel oak (*Quercus laurifolia*), sweet gum, elm, ash, and hackberry. The lower canopy averaged about 25 feet in height and was composed of saplings of the following species: sweet gum, red maple (*Acer rubrum*), laurel oak, water oak, swamp chestnut oak, hackberry, southern magnolia (*Magnolia grandiflora*), loblolly pine (*Pinus taeda*), American holly (*Ilex opaca*), red bay (*Persea borbonia*), and wax myrtle (*Myrica cerifera*). A heavy growth of lianas, including muscadine grape (*Vitis rotundifolia*), greenbriar (*Smilax* sp.), and rattanvine (*Berchemia scandens*), was distributed mainly through the lower canopy and added materially to the shading effect. The combined density of the upper and lower canopies was about 90 per cent.

The undergrowth, almost entirely scrub palmetto, averaged approximately three feet in height and was rather sparsely distributed — about 800 plants per acre on the sample area. (See Figure 5 for a photograph of Swainson's Warbler nesting in palmetto.)

Although there were some shallow pools beneath the palmetto, most of the ground was dry, or only damp, and had a light covering of leaves and other litter. The male Swainson's Warbler fed more often in the dry part of his territory than in the wet. For a short period one day I observed him wandering beyond the rather well-defined boundary of his territory, searching for food on a bed of dry loblolly pine needles.

Food Habits Related to Habitat

An analysis of the food from the stomachs of 10 Swainson's Warblers reveals the character of its foraging area and indicates that this species does most of its feeding on dry ground. The principal food items in the stomachs of four birds, collected in canebrakes, near the Fall Line in Georgia, were spiders and insects, mostly species inhabiting the ground rather than the foliage or water (Table 2).

My field observations corroborate these findings. By probing beneath leaves and drift debris lying on the ground the Swainson's Warbler finds most of the important invertebrates of its diet: spiders, ground beetles, crickets, and ants, as well as eggs, larvae, and pupae. The bird, therefore, forages mostly on the ground from where it also does much of its singing. And it may, at times, forage two or three feet, or slightly higher, in the undergrowth, probing into clusters of dead leaves and into the axils of cane plants like the Worm-eating Warbler (*Helmitheros vermivorus*). Occasionally, it flies from its perch in pursuit of insects.

Population Densities

From 22-27 April 1963, I observed four males singing daily in a 7-acre tract of cane, 3.5 miles southeast of Macon. In this same tract I had found three territorial males in April 1944 and five in April 1945. I counted 16 territorial males along a 2-mile transect through an extensive stand of cane, 5.5 miles southeast of Macon.

TABLE 2

Food of Four Swainson's Warblers from Georgia Canebrakes

Food items	*Per cent volume*	*Number times occurred*
Gryllidae	20.8	2
Undetermined insect fragments	12.6	3
Carabidae	8.2	2
Lepidoptera larvae	7.7	3
Acrydiinae	7.2	1
Formicidae	7.2	4
Arachnida eggs	7.2	1
Ichneumonidae	4.8	1
Hemiptera	4.3	3
Undetermined insect eggs	3.6	1
Undetermined insect larvae	3.0	1
Undetermined Coleoptera	2.4	1
Coleoptera larvae	2.4	2
Homoptera	2.1	2
Araneida	2.0	3
Cryptophagidae	1.0	1
Staphylinidae	0.7	1
Tenebrionidae	0.7	1
Hymenoptera	0.7	1
Tettigoniidae	0.5	1
Diptera pupae	0.5	1
Platygasteridae	0.2	1
Diplopoda	0.2	1

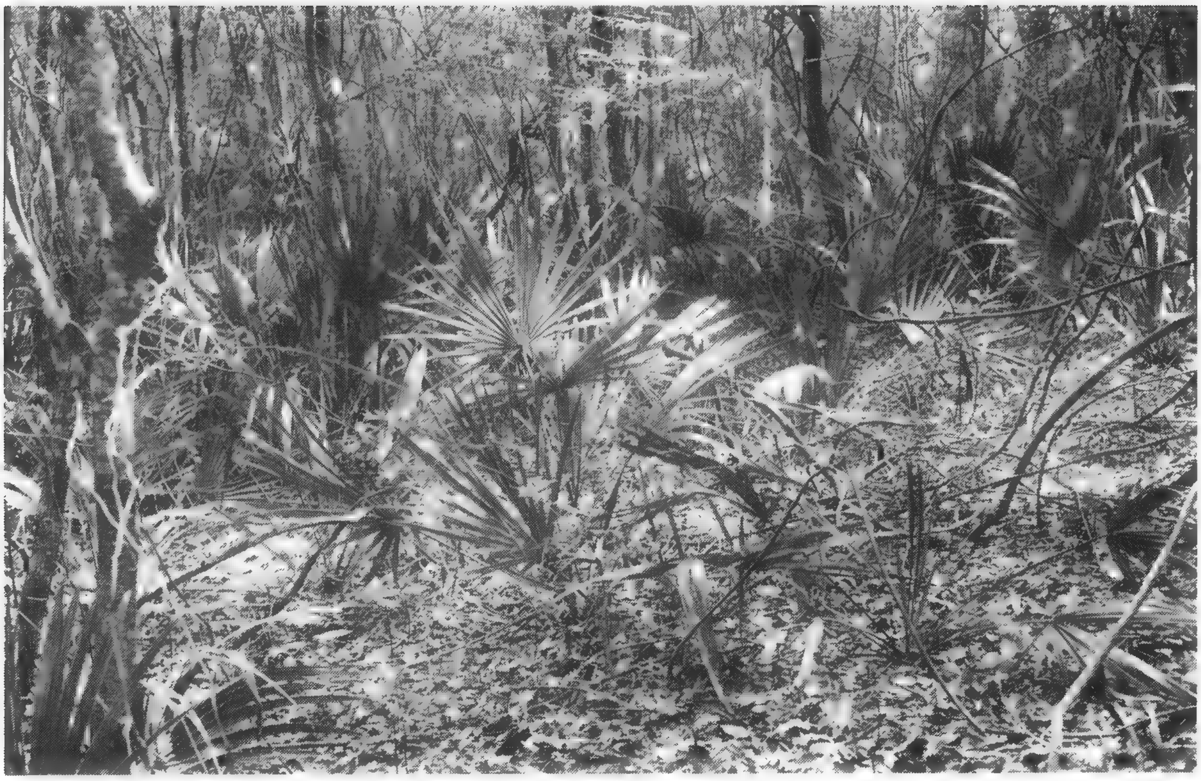


Figure 4. Part of scrub palmetto territory of Swainson's Warbler in Monkey John Swamp, Jasper County, South Carolina, approximately 10 miles north of Savannah, Georgia. May 1964.

In 1957, Norris (1963:47) studied the population densities in two forest types in the Savannah River Valley, Aiken and Barnwell Counties, South Carolina — an area approximately 25 miles south of the Fall Line. In his census areas he recorded seven adults per 100 acres in a floodplain forest; and four adults per 100 acres in a broadleaf deciduous, hammock-type forest that was especially rich in oaks. Both of these habitats contained scatterings of cane.

In a bottomland forest of the sweet gum-water oak type, with scrub palmetto undergrowth, in Rapides Parish, central Louisiana, April 1957, I noted a population density of 10 territorial males per 100 acres.

Along a 0.5-mile transect in the Dismal Swamp, Nansemond County, Virginia, 20 April 1958, R. E. Stewart and I counted eight territorial males, all of them in a swamp forest where red maple and tupelo gum formed the upper canopy and a light scattering of cane and white alder (*Clethra alnifolia*) made up the undergrowth.

Breeding Bird Associates of the Swainson's Warbler

A list of the species of birds breeding in association with the Swainson's Warbler is essentially the same in the two Coastal Plain habitats although each of these species seem to have a wider habitat tolerance than the Swainson's Warbler.

In the Ocmulgee River floodplain forest near Macon, the nesting species in closest association with the Swainson's Warbler were the Cardinal (*Richmondena cardinalis*), Hooded Warbler (*Wilsonia citrina*), and the White-eyed Vireo (*Vireo griseus*). All three nested in or on the edge of canebrakes as well as in other plant associations. The Cardinal fed mainly along the edge of cane thickets and in forest openings such as logging roads. The Hooded Warbler, which fed regularly from 2 to 30 feet above the ground, ranged through the more open growths of cane as well as the more open parts of the forest undergrowth. The White-eyed Vireos preferred mostly a less homogeneous habitat, more often the edge of viney thickets, and usually fed from 5 to 20 feet above the ground.

Other species, present in canebrakes but not so closely associated with the Swainson's Warbler, were the Carolina Wren (*Thryothorus ludovicianus*), Kentucky Warbler (*Oporornis formosus*), Rufous-sided Towhee (*Pipilo erythrophthalmus*), and Prothonotary Warbler (*Protonotaria citrea*). The Carolina Wren ranged throughout the floodplain forest, especially about old logs and brush piles. The Kentucky Warbler occurred most often where there was a denser ground cover, particularly of herbaceous plants, than in the canebrakes. The Towhee, a ground-feeder like the Swainson's and Kentucky Warblers, fed in the canebrakes but usually where the leaf litter and cover was thicker than in the areas used by the Swainson's Warbler. The Towhee also fed in other parts of the forest and in the edge of habitats. The Prothonotary Warbler preferred the banks of streams that flowed through the canebrakes and the vegetation along the banks.

During migration, Worm-eating Warblers and Ovenbirds (*Seiurus aurocapillus*) moved through the canebrakes as well as other parts of the floodplain forest.

Other Coastal Plain Habitats

Today in the lower Coastal Plain of Georgia and South Carolina, Swainson's Warblers also accept habitats where there is a scattering of cane in

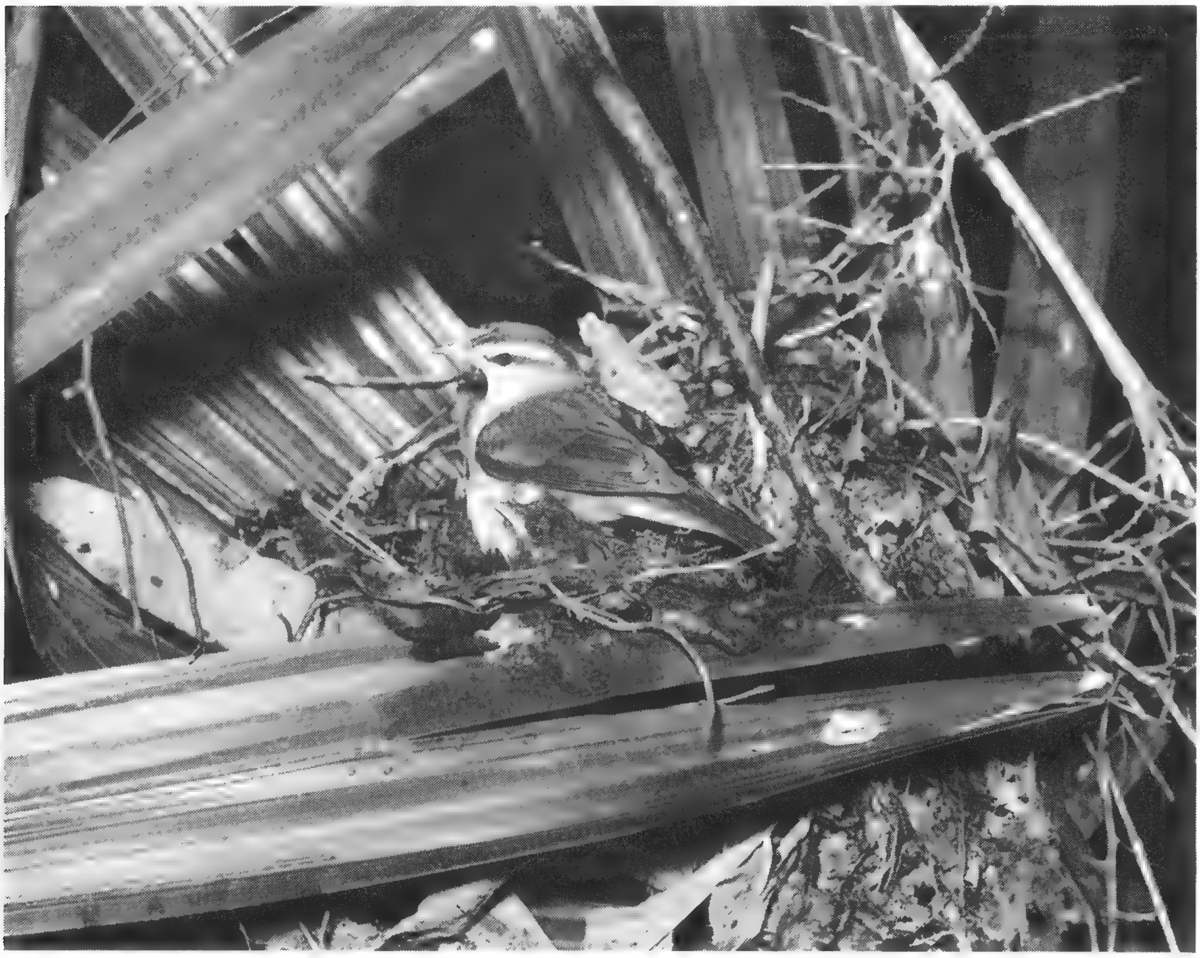


Figure 5. Swainson's Warbler nesting in scrub palmetto in the floodplain swamp bordering McGirt's Creek in south-central Duval County, Florida. The nest is shaded by a canopy mainly of ash and red maple. Photograph by Samuel A. Grimes.

branch bottoms (locally known as pineland galls or bay galls) that dissect the pine belt; in cypress bays; and, occasionally, in dry upland woods near the edges of swamps where there is no cane or scrub palmetto.

Wright and Harper (1913:485) and Wright and Wright (1932:137) described the cypress bay habitat of the Swainson's Warbler in the Okefinokee Swamp in Georgia. Its upper canopy is composed of pond cypress (*Taxodium ascendens*) and/or black gum (*Nyssa sylvatica*), with a scattering of slash pine (*Pinus caribaea*) and red maple; the lower canopy of saplings of the above, loblolly bay (*Gordonia lasianthus*), red bay, and swamp magnolia (*Magnolia virginiana*); the undergrowth of gallberry (*Ilex glabra*), fetterbush (*Lyonia lucida*), leucothoe (*Leucothoe racemosa*), and other shrubs; the ground cover of a number of ferns, including cinnamon (*Osmunda cinnamomea*), royal (*Osmunda regalis*), Virginia chain (*Anchistea virginica*), netted chain ferns (*Lorinseria areolata*), and several wetland plants. Sphagnum moss (*Sphagnum* sp.) carpets much of the cypress bay habitat. The authors failed to mention the leaf litter on top of the mossy carpet where the Swainson's no doubt spent most of its time. Habitats similar to the cypress bay exist elsewhere on the Coastal Plain. For example, in the Pocomoke Swamp, Maryland, at the northern limit of the breeding range of Swainson's Warbler on the Atlantic Coastal Plain, the life form of the plants and structure of the habitat is virtually the same; bald cypress replaces pond cypress, while other plant species such as black gum, red maple, swamp magnolia, leucothoe, and sphagnum persist.

Comparison with Mountain Habitat

The Swainson's Warbler is a locally common breeding bird in at least two major plant communities on the Allegheny Plateau of south-central and southwestern West Virginia. One is the rhododendron-mountain laurel-hemlock-American holly (*Rhododendron maximum-Kalmia latifolia-Tsuga canadensis-Ilex opaca*) plant community (Figure 6) near Mt. Lookout, Nicholas County, West Virginia, described by Brooks and Legg (1942). The other is the mature mountain cove hardwoods community (Figure 7) near Charleston, West Virginia, described by Sims and DeGarmo (1948).

In May and June 1965, I visited Charleston to study the mountain habitat of the Swainson's Warbler and to compare it with the habitat on the Coastal Plain. Charleston, on the Kanahwa River at an elevation of 600 feet, is in one of the warmest parts of the state and, that spring, the foliage was more advanced there than in Washington, D. C., which is on the inner edge of the Coastal Plain.

Most of the Swainson's Warblers occurred in the mountain ravines that lie at right angles to the river opposite the city; some of the areas were within two or three miles of the state capitol building. I found the birds at different elevations in these ravines. For example, in Donley Hollow, where I counted seven singing males along a one-mile transect on 15 May 1965, there were Swainson's Warblers on the floodplain of the stream (Donley Branch), on the benchland at the base of the steep mountain slopes, and on the slopes themselves. In most forests where the birds occurred, tulip poplar (*Liriodendron tulipifera*) was the dominant tree. The diameters-at-breast-height of the five largest tulip poplars in one breeding territory were 25, 30, 33, and 36 inches, respectively.

In one territory, that was on a benchland between Donley Branch and the mountain slope, the upper canopy had, in addition to tulip poplar,

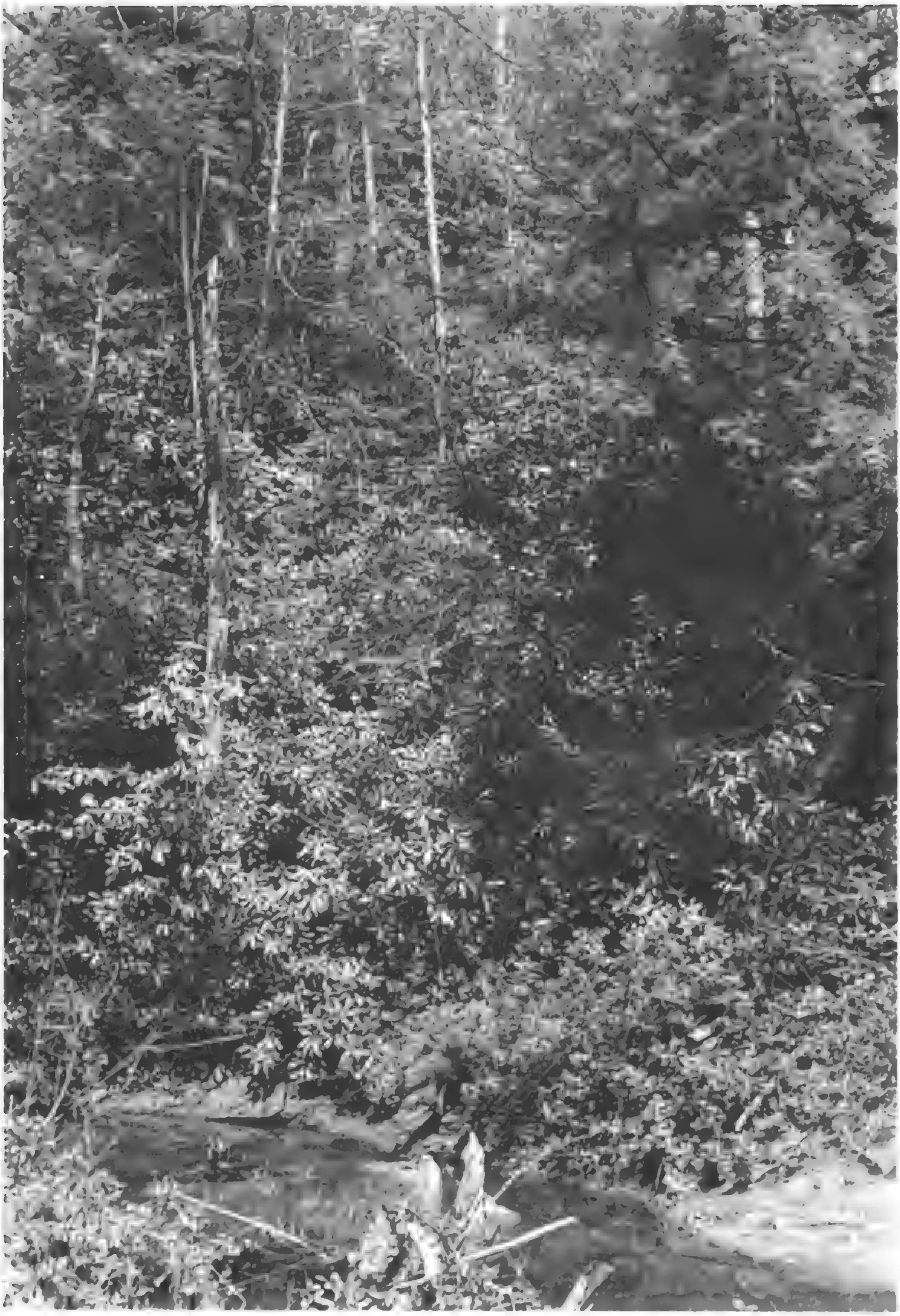


Figure 6. Mountain breeding habitat of the Swainson's Warbler along Collision Creek, on the Allegheny Plateau, Nicholas County, West Virginia. May 1966. In this habitat the Swainson's Warbler commonly selects rhododendron thickets.

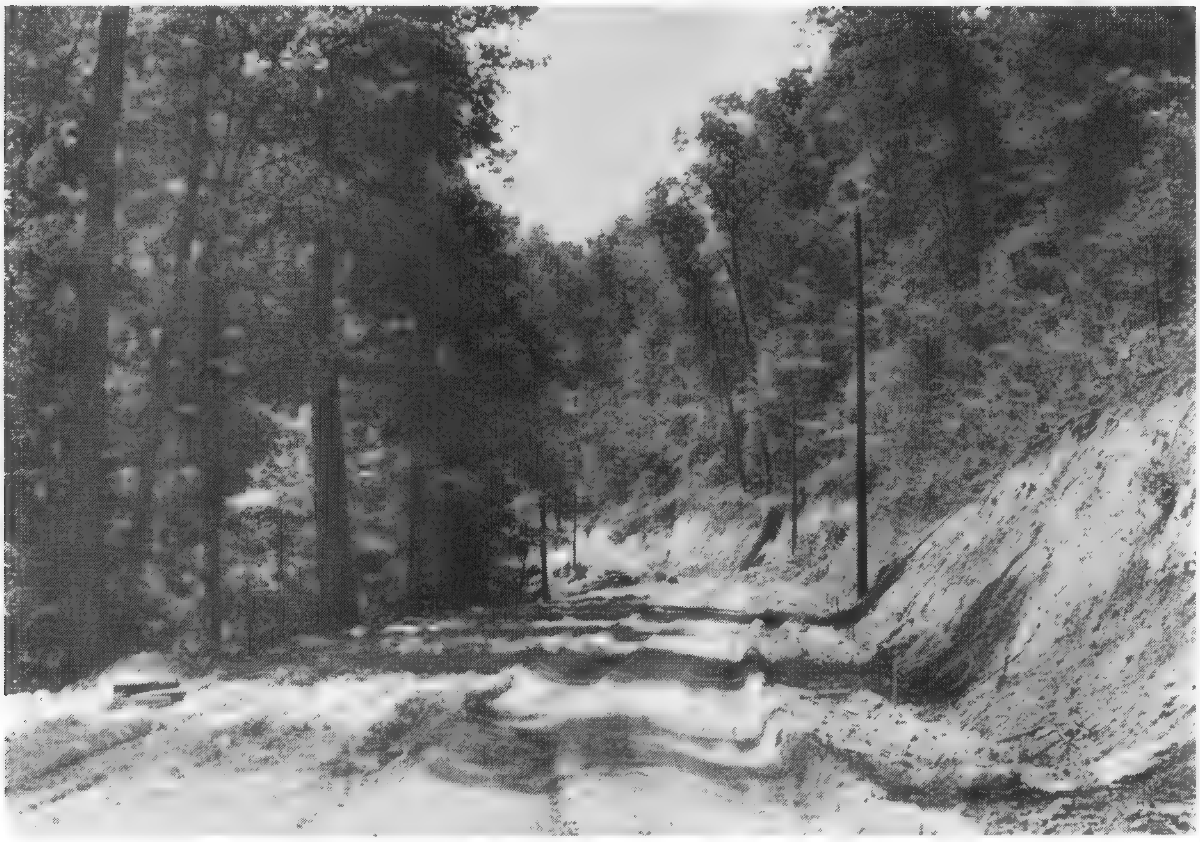


Figure 7. Mature mountain cove hardwoods habitat of Swainson's Warbler near Charleston, Kanahwa County, West Virginia. Tulip poplar is the dominant plant species. May 1965.

mainly black oak (*Quercus velutina*), buckeye (*Aesculus* sp.), red maple, and beech (*Fagus grandifolia*); near the stream side, sycamore (*Platanus occidentalis*) and sweet gum were dominant. Common smaller trees of the lower canopy were dogwood (*Cornus florida*) and umbrella magnolia (*Magnolia tripetala*). The undergrowth was mainly spicebush (*Benzoin aestivale*), pawpaw (*Asimina triloba*), and saplings of the tree species mentioned for the upper canopy. Occasional thickets of greenbriar (*Smilax* sp.) and honeysuckle (*Lonicera japonica*) occurred in the undergrowth. Prominent ground cover plants in the territory were May apple (*Podophyllum peltatum*), nettle (*Laportea canadensis*), violet (*Viola* sp.), baneberry (*Actaea* sp.), and Christmas fern (*Polystichum acrostichoides*).

In another Swainson's territory, in a flatland area along a stream, the woods had the appearance of a miniature floodplain forest of the Coastal Plain and was not unlike the habitat occupied by this bird in the batture (land between the levee and river) of the delta land near Rosedale, Mississippi. Sycamore was the dominant tree of the upper canopy, with elm (*Ulmus* sp.), tulip poplar, and red maple also present. The common plants of the undergrowth were spicebush, elderberry (*Sambucus* sp.), and pawpaw interspersed with entanglements of smilax, grape (*Vitis* sp.), and briar (*Rubus* sp.). The plants in the ground cover included nettle, poison ivy (*Toxicodendron radicans*), and jewelweed (*Impatiens pallida*).

In the mountain habitat at Charleston, as in those of the Coastal Plain, Swainson's Warblers occur mainly in medium dense undergrowth and only rarely in the densest thickets of heavy viney growth or blackberry patches. One rather unique feature of the Swainson's habitat at Charleston is that one may walk through it with relative ease. Also, normally the cover on the ground where the birds feed is moderately well covered with herbaceous plants.

As in the canebrake habitat in central Georgia, its closest avian associates in the mountain habitat include the Kentucky Warbler, Hooded Warbler, Cardinal, Rufous-sided Towhee, and White-eyed Vireo. Others present in the mountain habitats are the Black-and-white Warbler *(Mniotilta varia)*, Worm-eating Warbler, and Ovenbird.

Twelve Weston exposure meter readings at Swainson's Warbler feeding sites in Donley Hollow ranged from 13 to 150 with an average of 47.

Discussion

In most parts of its breeding range the Swainson's Warbler prefers mature river forests or mature forests not far from rivers or their tributaries. Although this bird occasionally occurs where the ground is swampy or boggy, deep shade, moderately dense undergrowth, and dry land are generally characteristic of most of its breeding habitat. Herbaceous vegetation is usually absent from its nesting territories in the Coastal Plain habitats as well as in some of its mountain habitats. A rather sparse undergrowth and ground cover would seem to fit its quick feeding motion on the ground. A thin or rather flat leaf litter also seems to be suited to its rapid and erratic manner of movement.

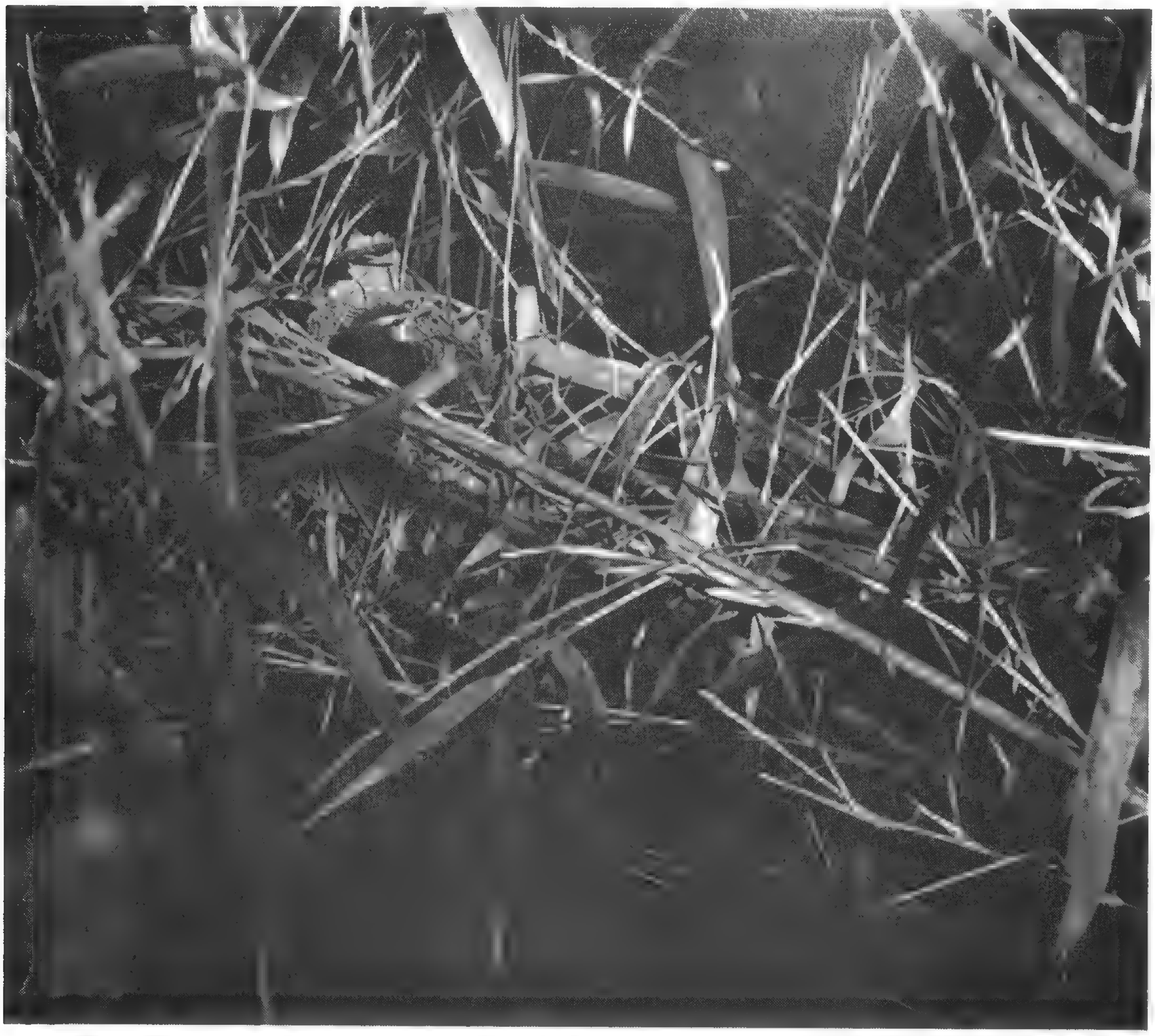


Figure 8. Swainson's Warbler incubating during flood stage in Ocmulgee River floodplain forest, Macon, Georgia. May 1946. Water is three feet deep.

There appears to be a misconception regarding the density of the habitat occupied by the Swainson's Warbler. In some habitats, for example, the cypress bay, the general aspect or structure of the area may be extremely dense and seemingly impenetrable by a human being. The undergrowth may be a jungle-like mixture of greenbriar and ericaceous shrubs. However, the Swainson's Warbler niche in this extremely dense undergrowth is usually where the shrubs are the least dense and in small openings between clumps of greenbriar or various other forms of undergrowth.

Early workers on the Coastal Plain usually associated the Swainson's Warbler with wetland situations, inferring that it occupied a niche somewhat like the Louisiana Waterthrush (*Seiurus motacilla*). However, when a Swainson's Warbler selects a low-lying territory in a river bottom or a floodplain forest, it chooses that portion where the ground is usually dry, and which, because it is low-lying and subject to slow drainage, may become a temporary wetland after a heavy rainfall.

When the periodic flooding associated with river floodplain forests occurs during the nesting season (Figure 8), the effect on the breeding populations of the Swainson's Warbler is devastating. The canebrakes on the river side and along the tributaries of the river are the first areas to be flooded and remain flooded the longest.

An inundation of the nesting grounds is more devastating to populations of the Swainson's Warbler than to populations of the other species that nest in the canebrakes because Swainson's Warblers rarely nest elsewhere than on floodplains. Other species that nest in the canebrakes also nest on the upland side of the bottomland.

When I arrived at the Ocmulgee River floodplain forest a few miles south of Macon, Georgia, on 30 April 1964, almost the entire area was flooded. My former study area was under six feet of water. By May 14 most of the water had receded, but where there had been four territorial males at that time the previous spring, I neither heard nor saw a Swainson's Warbler. Since nesting begins during the first two weeks in May, and the height of the average nest is four feet, productivity is certainly lower under conditions of extreme flooding.

Summary

The Swainson's Warbler (*Limnothlypis swainsonii*) is a local breeding bird of the South Atlantic and Gulf Coastal Plains, the southern Appalachians northward into West Virginia, and occasionally the southern Piedmont Plateau. The purpose of this paper is to present a more exact evaluation of features of the breeding habitat, already generally described.

In the Coastal Plain of Georgia and South Carolina, there appears to be a correlation between the breeding density of Swainson's Warblers and the distribution and extent of canebrakes. Most of these warblers occur in the most extensive canebrakes in the river floodplain forests of the upper Coastal Plain, usually near the Fall Line. In an optimum habitat, they are in small groups, such as are characteristic of Kirtland's Warblers. At the turn of this century Swainson's Warblers were apparently more numerous in the lower Coastal Plain than they are today. Most of my recent observations on Swainson's Warblers in the lower Coastal Plain of Georgia and South Carolina revealed widely scattered bachelor males, in contrast to nesting pairs found in the upper Coastal Plain, an indication that today most habitat on the lower Coastal Plain is marginal.

I have described the floodplain forest-canebrake habitat of the upper Coastal Plain, near Macon, Georgia, and the swamp forest-scrub palmetto habitat near Savannah, Georgia; compared these with the mature cove hardwoods mountain habitat near Charleston, West Virginia; and given population densities and breeding bird associates.

The general characteristics of most of the breeding habitat pointed up the need of the bird for deep shade, moderately dense undergrowth, and dry land within the river floodplain forest.

The periodic flooding of river floodplain forests of the Coastal Plain during the nesting season may have a devastating effect on breeding populations.

Acknowledgments

I am grateful to Robert T. Mitchell of the Patuxent Wildlife Research Center for the identification of contents of several Swainson's Warbler stomachs; and to P. A. Stewart of the same institution for reviewing the manuscript.

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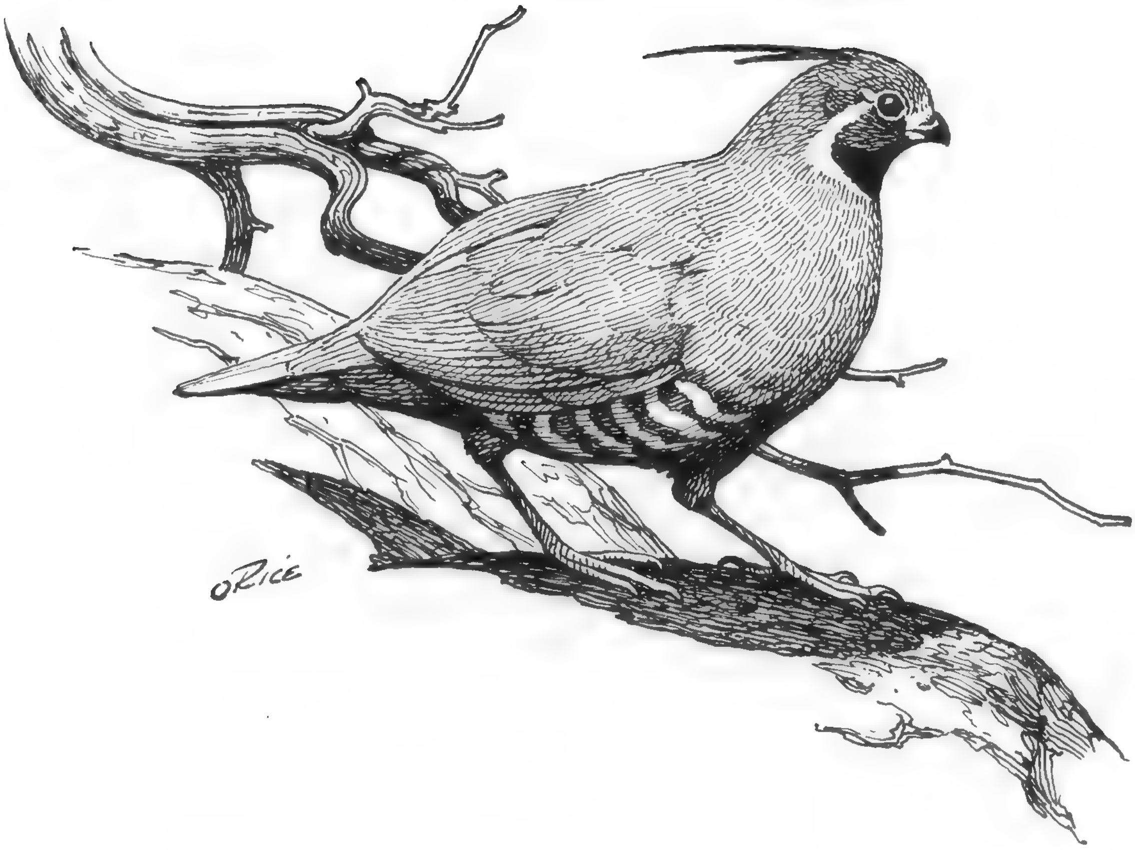

Mountain Quail, *Oreortyx pictus.* Drawing by Orville O. Rice.

HEARING LOSS AND BIRD SONG

Harold Mayfield

Audiospectrograms, courtesy of Donald J. Borror, Ohio State University

Most of us take for granted that we will wear reading glasses in middle and later life. We may not be so well aware, however, that parallel changes take place in the ear and affect our hearing as we grow older. The change in our eye we note almost immediately, because it affects an ability we use all of the time, the ability to focus on close objects. But the change in our ear we may not notice for many years, because it affects at first only our ability to hear sounds of very high pitch, leaving unchanged our perception of lower tones in the "useful" range of conversation and most of the familiar sounds of our environment.

Very few people will recognize the early changes in their hearing without an audiometric examination. The exception is the bird watcher. He is "testing" his ears constantly by identifying bird songs and calls, many of them musical tones at characteristic, high frequencies. When he loses a little of his hearing range, he loses the songs of certain species. Hence, hearing loss takes on special interest to the bird watcher.

Sound and Hearing

The air is an elastic medium that quivers like gelatin. A vibrating body in air pushes and pulls it, generating waves of compression and rarefaction that radiate outward at the speed of sound. As these waves pass any point, they are detectable as slight rhythmic changes in air pressure. Parts of the ear are attuned to vibrate with these changes in pressure; and if the intensity is great enough and if the frequencies are within certain limits, the vibrations are recorded on the brain as sound. Pure tones are produced by a single train of waves of one frequency; but most of the sounds we hear are complex mixtures of such tones. Most young adult human beings can hear frequencies as low as 16 cycles per second and as high as 16,000 cps, with a few hearing up to 20,000.

The human ear is most efficient between 1,000 and 4,000 cps; that is, sounds below or above this range must be more intense to be heard.

Therefore, the human ear detects only a part of the sound generated in nature, missing all that is too low or too high in frequency or too low in intensity to actuate the mechanism of the ear. Some other mammals can hear sounds that are a little lower in intensity and higher in frequency than those audible to us.

Familiar examples are the dog, whose hearing sensitivity is legendary and whose high-frequency range is attested by the existence of "silent" dog whistles. The bat is famous for its ability to sense objects in the dark with a sonar system of calls and echoes pitched mostly too high for the human ear. The hearing range is known for only a little more than a dozen species of birds, but the scanty evidence at hand suggests that the range of birds generally is much less than of mammals. For example, the range of man is about ten octaves (16-16,000 cps), whereas the range of the Starling (*Sturnus vulgaris*) is less than five octaves (700-16,000 cps). It is surprising that birds, with their high-pitched voices and small ear mechanisms, do not hear sounds of higher frequency than we do. The highest upper limits demonstrated in birds are very close to highest for man, about 20,000 cps, and not all species do so well. Birds, however, do not hear sounds low on the scale nearly as well as we do. Probably few if any small song birds hear as low as the middle of the piano keyboard (Schwartzkopff, 1955:341; Frings and Slocum, 1958: 100). Field students have remarked that a bird may seem startled at the soft snapping of a twig but oblivious to the murmured voice of a man.

Frequency, Intensity, and Quality

The frequency of sound is measured in cycles (vibrations or waves) per second. The frequency determines the pitch of musical tones. For example, the frequency of middle C is 256 cps; the C an octave below is 128 cps, and the C an octave above middle C is 512 cps. Thus, each corresponding note in the next higher octave has twice the frequency. The highest note on the piano keyboard, four octaves above middle C, has a frequency of 4,096 cps. These are the conventional figures of the physicist; musicians use slightly different frequencies for the recognized musical scales.

The average frequency of the songs of passerine birds is about 4,280 cps, which is about an octave and a half above the highest note a coloratura soprano can sing. Of course, the songs of some species are pitched much higher than others. The average of the wood warblers is about 5,350 cps and of the thrushes, 2,890 cps which is just below the highest F sharp on the piano. These averages give a general impression of the pitch of some familiar birds, but they should not cause one to forget that one song may have a wide range of frequencies. For example, the range for the Catbird (*Dumetella carolinensis*) is 1,100-4,375; Robin (*Turdus migratorius*), 2,200-3,300; Red-eyed Vireo (*Vireo olivaceus*), 2,375-5,850; Blackpoll Warbler (*Dendroica striata*), 8,050-10,225; Ovenbird (*Seiurus aurocapillus*), 3,300-5,850; Western Meadowlark (*Sturnella neglecta*), 1,475-3,475; Cardinal (*Richmondena cardinalis*), 2,200-4,375; Song Sparrow (*Melospiza melodia*), 1,900-7,700 (Brand, 1938:263-268). With larger samples and more refined equipment, Borror and Gunn (1958) and Borror (1961) found the range for the Ovenbird, 2,500-9,000; Cardinal, 1,500-4,500; and Song Sparrow, 1,800-9,000.

For measuring the loudness or intensity of sound, a different kind of unit is used. The differences to be measured are much greater than our hearing would lead us to suppose, for our ear perceives one sound as only a little louder than another when its power may be actually much greater; that is, our perception of sound varies in logarithmic relation to its actual power. Therefore, the intensity of sound is measured on a logarithmic scale. The unit is the decibel (db). But this is not a quantity; it is a ratio on a logarithmic scale between a measured quantity and a reference quantity. The ratio may be of two amounts of sound power, in which case the reference is 10^{-13} watt, or of two sound pressures, where the reference pressure is taken as 0.000,2 microbar (the same as 0.000,2 dynes per square centimeter).

Decibels cannot be added by simple arithmetic. One decibel difference (a change barely perceptible to the human ear) at low levels of sound may represent a very little difference in power, and one decibel at high levels of sound may represent a very large difference in power.

If two sounds of the same intensity are added to one another, the increase is three decibels, whether the sounds are very faint or very strong. Since the intensity of sound decreases with the square of the distance (in a free field, where the effects of boundaries and reflections are negligible), doubling the distance from the source of a sound reduces its intensity by six decibels.

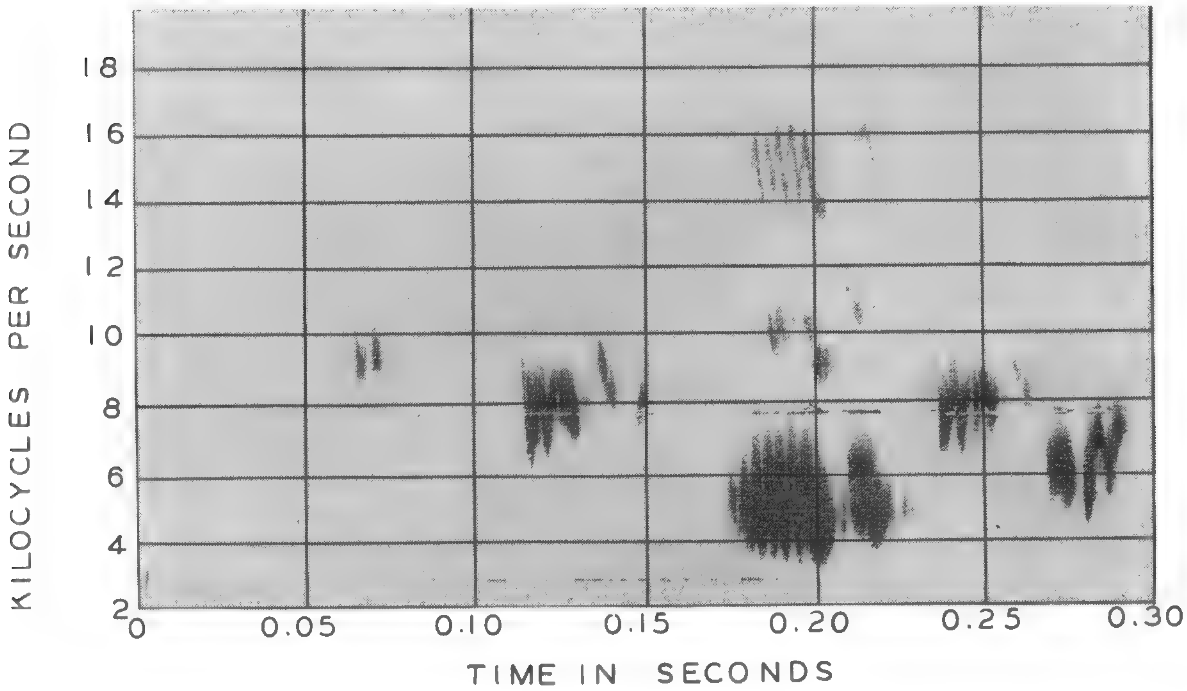

Figure 1. Audiospectrogram of the song of the Henslow's Sparrow. This unmusical vocal effort suggests to the human ear something like "k-slick." Note that the whole song lasts only about one-fourth second, and the central explosive note reveals two harmonic overtones.

Some illustrative sound pressure levels are as follows: permissible background level in a broadcasting studio, 25-30 db; average residence, 40-45 db; private business office, 50 db; accounting office, 55 db; conversational speech at three feet, 60 db; auto passing at twenty feet, 75 db; inside a closed car in city traffic, 90 db; boiler shop, 125 db.

In addition to frequency and intensity, another distinguishing factor in sounds is their quality, often called timbre in music. This is the factor that allows us to distinguish between different musical instruments (or birds) even though they are emitting notes of the same pitch and loudness. It comes from the mixture of frequencies. The timbre of a musical tone comes from the admixture with the fundamental frequency of higher frequencies (overtones). Hardly any instrument (or bird) emits a pure tone, and the possible variations of mixture are infinite. If the extra frequencies are strong and inharmonious, we describe the note as buzzy, sibilant, hoarse, or some other word implying it is nonmusical. If the note is so mixed that we cannot ascribe a pitch to it, we call it a noise rather than a tone. The explosive notes of some of the flycatchers are of this kind, as is the song of the Henslow's Sparrow (*Passerherbulus henslowii*) shown in the audiospectrogram of Figure 1.

Sometimes an equivalent effect may be produced not by mixing frequencies but by slurring—that is, by sliding from one frequency to another so rapidly that the ear does not separate them, just as the eye merges two images presented rapidly in succession. An example is the song of the Chipping Sparrow (*Spizella passerina*) in Figure 2.

Modulation of the frequency (rapid up-and-down fluctuation of the frequency) gives a hissing quality, usually described *zee-zee-zee* as in the song of the Cape May Warbler (*Dendroica tigrina*) shown in Figure 3.

I am not considering tone quality further in this paper except to point out that declining sensitivity to the higher frequencies will cause our perception of the quality of bird song to change. But since such impressions are entirely subjective, we will not be aware of a change in our perceptions except perhaps through memory or discussions (arguments?) with our friends about what they are hearing.

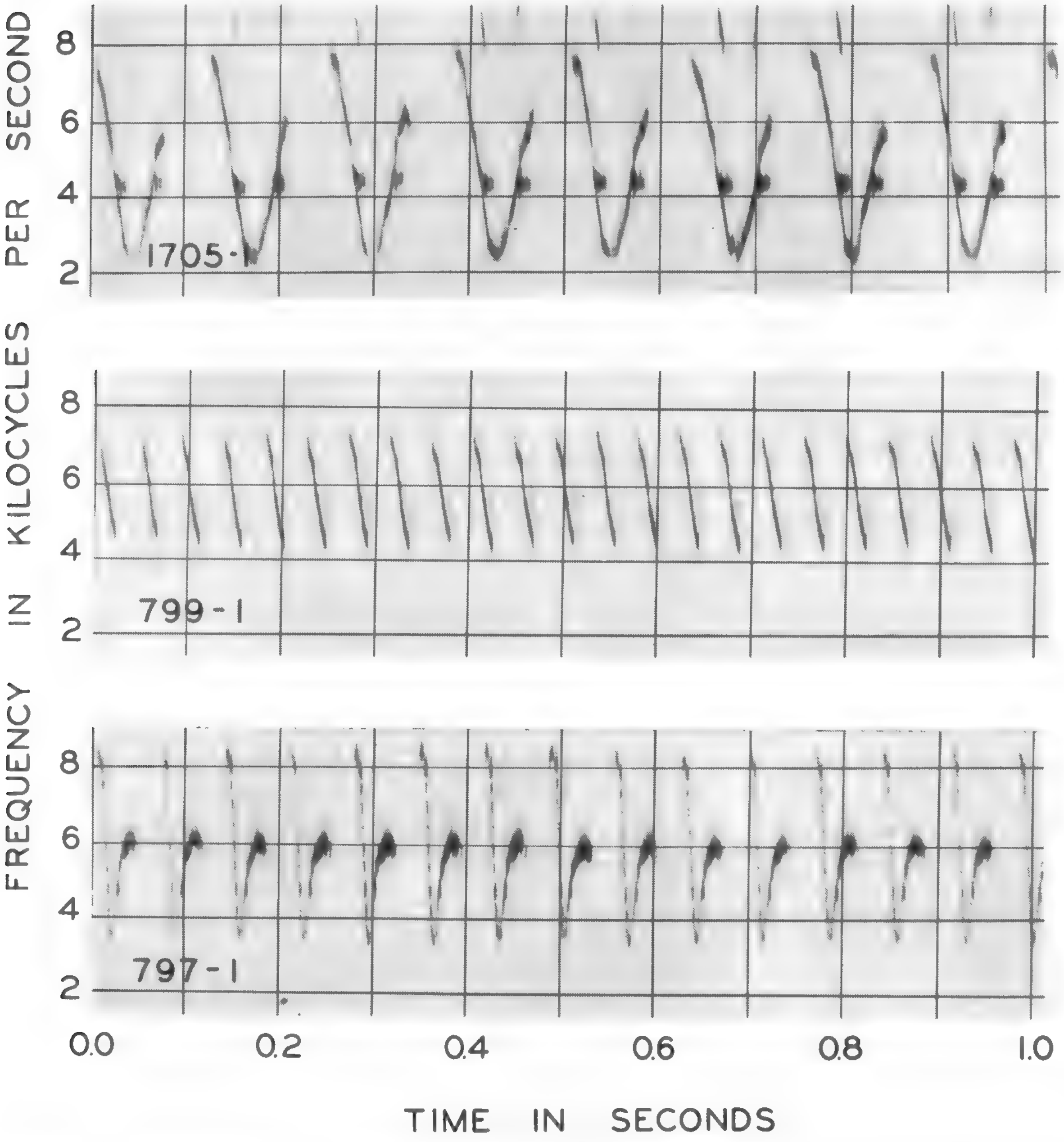

Figure 2. Audiospectrogram of songs of the Chipping Sparrow shows how slurring of notes can destroy perception of pitch. The downslurs sometimes cover more than an octave, and in song 797-1 particularly, each downslur is very rapid, requiring about 1/100 sec. The effect is a non-musical, machine-like trill.

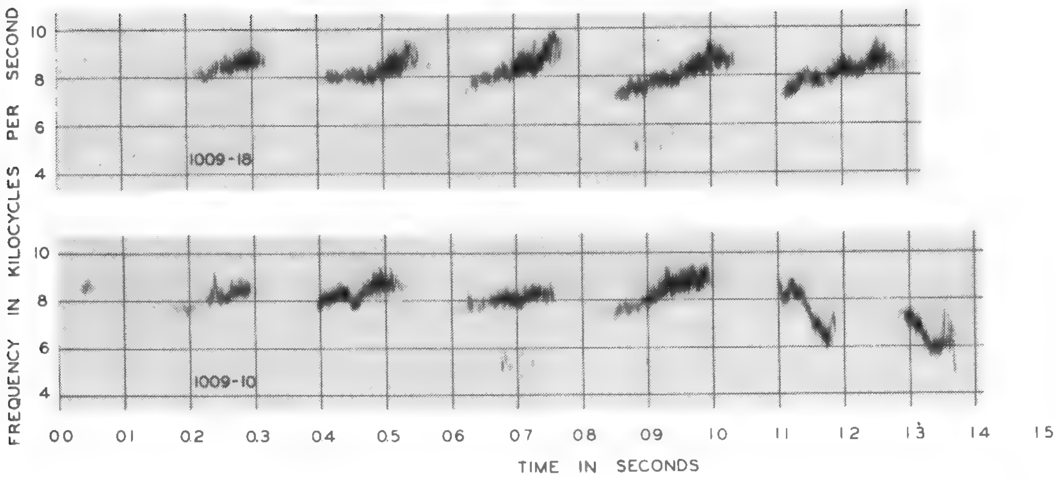

Figure 3. Audiospectrogram of songs of the Cape May Warbler. The rapid up-and-down changes in frequency (modulation) are heard by the human ear as a hissing or sibilant quality sometimes described as, "zee, zee, zee . . ."

Hearing Loss with Age

There are many diseases that can affect the auditory system, but even if we escape all of them, there are two sources of injury that are virtually inevitable: first, the effect of *aging* and, second, *trauma* from a noisy environment.

The hearing loss from age alone is called presbycusis, corresponding to presbyopia that causes us to don reading glasses in middle age. Statistically, a distinct worsening in hearing can be detected in a population of men at about 32 years of age, and among women at about 37. Here as in so many other instances the supposedly more delicate sex proves to be the more enduring. On the other hand, although this superiority of women in perception of high notes persists, their ability to hear lower notes declines more rapidly than men and by their mid-fifties women hear no better than men at the frequencies needed to understand conversation (Corso, 1962:21, 25, 29).

At first this change affects only our ability to hear the very highest frequencies audible to us in youth. Gradually it spreads into the lower frequencies. For example, about half of all men in their mid-forties show a slight but significant loss in sensitivity to pure tones at 4,000 cps and higher; whereas the majority of men do not show any significant decline in ability to hear pure tones at 1,000 cps (almost two octaves above middle C) until they are in their seventies (Corso, 1962:24).

In addition to the inexorable advance of age, we also suffer from the wear and tear of a noisy civilization. Everyone is aware of the more spectacular abuses to human hearing — artillery fire, jet engines, the proverbial boiler factory — but most of us are oblivious to the customary din about us. The city dweller scarcely notices the roar of city traffic; the farmer doesn't think about the clatter of his tractor, although he must shout at the top of his lungs to be heard above it. Yet, all this pounding on the auditory system eventually takes its toll on people who are sensitive to it, and for those in some occupations this toll may become serious early in life. Damage from noise exposure, as distinct from the usual processes of aging, typically appears first in our sensitivity to tones at about 4,000 cps, and then spreads into the higher and lower frequencies.

Hence, damage from noise affects us *first* almost exactly at the frequency band of the average songbird voice but not in the band of our "useful" hearing. For the ordinary purposes of life the frequencies below 2,000 cps are most important, because this is the range needed to understand conversation—and indeed to hear most of the sounds around us, including enough of music to enjoy it.

My own interest in this subject derived initially from my work in industry, where I am concerned with the effects of noise and the prevention of it. I came to realize that the bird watcher has a special concern for this problem some years ago as I was guiding a group of gray-haired people on a field trip. I had stopped our cars at a roadside to point out a Grasshopper Sparrow (*Ammodramus savannarum*) singing from a fence wire. Gradually it dawned on me that several of the people did not know where to point their binoculars. A quick poll showed that less than half of them could hear the bird. The notes of the Grasshopper Sparrow are pitched very high, from 7,600 to 9,500 cps.

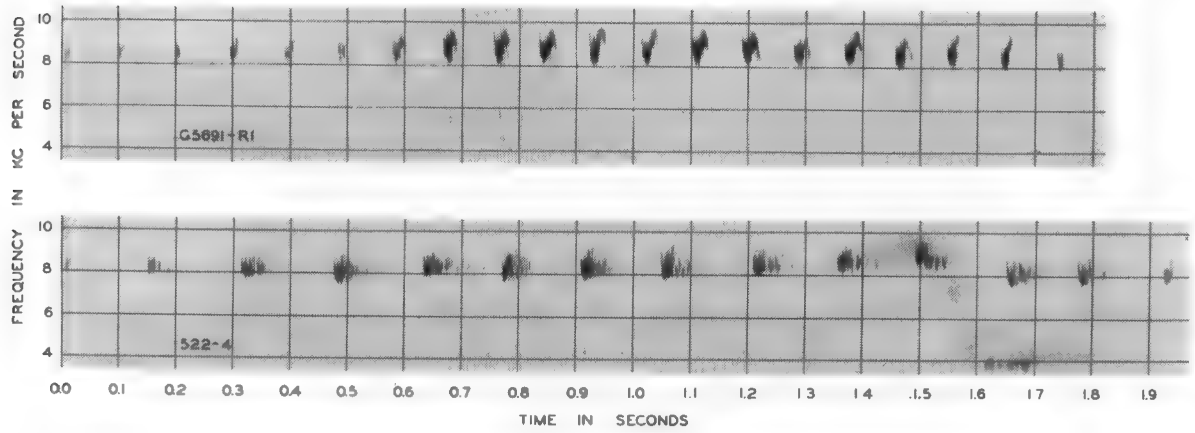

Figure 4. Audiospectrogram of the songs of two individuals of the Blackpoll Warbler. Typically the song consists of a rapid series of notes on one pitch, starting softly, increasing in volume, and then dying off at the end. The entire song is usually above 8,000 cycles per second.

This same sparrow's song was singled out by the late William E. Saunders (1934:503-506) as one of the best indicators of hearing loss, although Saunders recognized that he had lost the songs of several warblers earlier, and first of all at 60, the faint call notes of the Golden-crowned Kinglet and Brown Creeper (*Regulus satrapa* and *Certhia familiaris*). Another song entirely of very high pitch is the Blackpoll Warbler whose audiospectrogram is shown in Figure 4.

To imply that a bird song is suddenly lost through age is misleading. Our ability to hear the higher frequencies does not wink out like a light. Rather, the threshold of hearing gradually rises, and a higher intensity becomes necessary to actuate our ear mechanism. As long as the threshold increase is less than 15 db, the loss in sensitivity is not considered significant. By convention, a rise in threshold of 15-30 db is considered a slight loss; 30-45 db, mild; 45-60 db, marked; 60-80 db, severe; and 80 db, extreme.

So a person probably will lose the ability to hear certain bird songs at a distance long before he loses them close up. But not many people will be aware of any change until they see a bird fairly close at hand with its bill moving in unmistakable song but without any sound coming forth.

Even here most songs are not likely to be lost totally. The more accomplished songsters give forth a variety of notes that are by turns soft and loud in volume and high and low in pitch. Consequently, a person at first loses only those parts of the song that are both high and soft. Thus, he still hears and recognizes the song, but may or may not be aware that a part of it is missing. (Many hi-fi enthusiasts go to great lengths to produce frequencies they cannot hear.) Some of our disagreement in describing bird songs may arise from such differences in perception. Some of us actually hear elements of a song that others miss.

Saunders at age 71 could hear a Black-throated Green Warbler (*Dendroica virens*) plainly at 25 yards, but he missed its final note which his brother heard plainly. He judged, probably correctly, that the problem in this instance was the lower volume of that note rather than higher pitch.

However, all is not gloom in this partial loss of auditory sensitivity. Saunders found that the screening out of high-pitched sounds actually had the effect of sharpening his perception of some lower notes, such as the call note of the Purple Finch (*Carpodacus purpureus*).

Bird Song Intensities at Screened Frequencies

Exact measurements are available for the *frequency* and *tempo* of many bird songs (Brand, 1938; Borror and Gunn, 1958; and Borror, 1961, 1964), but I find no published information on the *loudness* of bird songs expressed in conventional intensity measurement units. Therefore, I am presenting some sound pressure levels (see Table 1) delivered by four species from different families that were accessible to me for deliberate observation: House Wren (*Troglodytes aedon*), Warbling Vireo (*Vireo gilvus*), Golden-winged Warbler (*Vermivora chrysoptera*), and Field Sparrow (*Spizella pusilla*).

The instrument was a Bruel and Kjaer precision sound level meter, Type 2203, with condenser microphone Type 4131, and with octave filter set, Type 1613, giving selectively the sound pressure levels for the octave bands centering on 31.5, 63, 125, 250, 500, 1,000, 2,000, 4,000, 8,000, 16,000, 31,500 cps. On this instrument decibels are read visually from a needle on a dial.

Since I was interested primarily in human perception of bird song, where so much depends on frequency, I concentrated my attention on the sound pressure level at stated octave bands rather than on the total or over-all sound pressure level. In each of the species studied I found that the song revealed much more energy in one octave band than in any other. This I have called the dominant octave band. Typically, a bird showed strong volume in one band and a much weaker volume in the adjacent band above or below it. Any elements of song outside the bands adjacent to the dominant band were not strong enough to be distinguished from the background noises.

Since a song usually consists of a series of bursts varying widely in frequency and intensity, the needle of the sound level meter fluctuates rapidly, and there is a question about which number to regard as the best measure of the song's loudness and also whether the peak needle excursion fully measures the "burst" or impulse noise. Therefore, I did not use the extreme swing of the needle but rather attempted to identify the highest point at which the needle held steady momentarily or to which the needle returned repeatedly. This is like trying to assign a height to a group of trees; is it the height of the tallest tree or the approximate height of several of the tallest? I have chosen the latter point of view.

In each of these examples, one bird supplied all of the songs, but the deflection of the needle was watched for dozens of times to select a typical reading. Each usable series of songs was uttered from one location without intervening limbs or other obstructions. The House Wren was near its nest about 1.5 meters from the ground, the Warbling Vireo was on its nest about 7 m from the ground, the Golden-winged Warbler was on a song perch about 8 m above the ground, and the Field Sparrow was on a song perch about 2 m from the ground. The sound level meter was on a tripod about 1 m from the ground and pointed toward the bird. All measurements of sound pressure level are in decibels *re* 0.000,2 dynes per square centimeter (the conventional reference point for most decibel scales used in acoustical work).

TABLE 1

Sound Pressure Levels of Bird Song

Species	*Decibels by octave bands*[1]			*Distance*
House Wren	50 db (4,000 cps)	44 db (8,000 cps)	40 db (2,000 cps)	19 m
Warbling Vireo	52 db (4,000 cps)	43 db (2,000 cps)		15 m
Golden-winged Warbler	53 db (8,000 cps)	45 db (4,000 cps)		23 m
Field sparrow	52 db (4,000 cps)	35 db (2,000 cps)		18 m

[1] These are not pure-tone frequencies but octave-wide bands centering on the frequencies shown.

In the elaborate song of the House Wren, it was apparent that the loudest part of the song at the 4,000 cps octave band occurred in the middle, whereas the loudest part at the 2,000 cps octave band occurred near the end where the pitch dropped noticeably. Thus, if a person did not hear well in the 4,000 cps octave band, the pattern of the wren's song would be quite different although he might still hear it well.

The songs of these four birds are pitched mainly in the octave bands centering on 4,000 and 8,000 cps, as are those of many other small songbirds.

TABLE 2

Median Hearing Thresholds of Human Ear in Decibels by Age Groups[1]

Frequency in cps	*Sex*	*43 to 49 years*	*51 to 57 years*	*59 to 65 years*
1,000	Male	5.5	10.9	13.6
	Female	5.9	12.7	11.8
2,000	Male	14.0	14.6	22.9
	Female	11.4	17.5	17.7
4,000	Male	32.0	26.8	48.8
	Female	15.8	21.7	25.9
8,000	Male	36.0	42.0	57.2
	Female	25.8	34.0	41.8

[1] This sample consisted of people in the United States with no history of ear disease nor of exposure to excessive noise. The thresholds are for pure tones at the frequencies stated (Corso, 1962:41).

However, some birds have voices of much lower pitch; for example, I found the voice of the Mourning Dove (*Zenaida macroura*) mainly in the octave band centering on 500 cps.

The median thresholds in Table 2 are above the sound pressure levels produced by the songbirds in Table 1 only for the 59-65-year age group and the Golden-winged Warbler. Generalizing, I suggest tentatively that various small songbirds produce sound pressure levels in their dominant octave bands of about 50 decibels at a distance of 20 meters. Because of the effects of presbycusis, less than half of all men between ages 59 and 65 with otherwise relatively healthy ears will hear those birds whose songs are pitched mostly in the octave band centering on 8,000 cps.

Summary

Human ears, even in the absence of disease or violent injury, tend to lose sensitivity with advancing age. The change, beginning in men as early as 32 years, at first affects only the frequencies at the upper end of the hearing spectrum and would seldom be noticed except by bird students, who are constantly "testing" their ears against bird songs of very high pitch. Since a bird song may include a variety of frequencies and intensities, a decline in sensitivity at the higher frequencies may change one's perception of the song long before the song is totally lost. Each of four songbirds—House Wren, Warbling Vireo, Golden-winged Warbler, and Field Sparrow—was found to have its greatest intensity in one of the two octave bands centering on 4,000 or 8,000 cycles per second. At their dominant octave bands the sound level pressures of all were about 50 decibels at a distance of 20 meters. Comparison with data on hearing thresholds of people at various ages suggests tentatively that less than half of men 59 to 65 years of age will be able to hear at 20 meters the Golden-winged Warbler and other birds whose voices are pitched mainly in the octave band centering on 8,000 cycles per second.

Acknowledgments

I wish to express thanks to two friends who read an earlier draft of this manuscript and criticized it helpfully, Donald J. Borror, on questions of bird song, and Willis G. Hazard, on the physics of sound.

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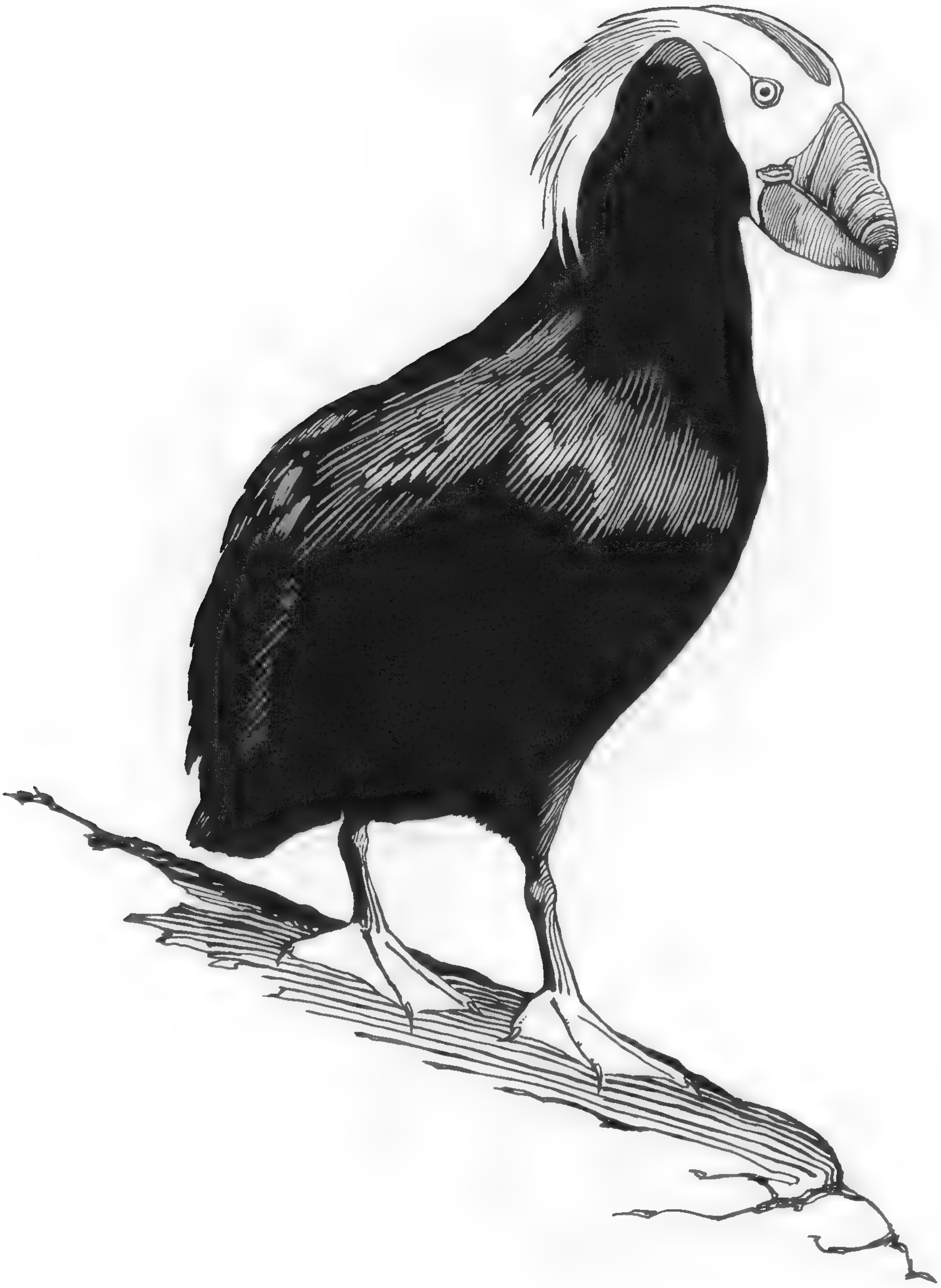


Tufted Puffin, *Linda cirrhata*. Drawing by George Miksch Sutton.

GROUND-NESTING GREAT HORNED OWL: A PHOTOGRAPHIC STUDY

FREDERICK KENT TRUSLOW

Photographs by the author unless otherwise indicated

On 21 December 1964, Mr. George Harmon found a nest of the Great Horned Owl (*Bubo virginianus*) in a 15-acre woodlot of slash pine about 2.5 miles from Homestead, Florida. The nest, containing two eggs, was on the ground in a fairly dense stand of palmetto that averaged three feet in height and under pines that were from 35 to 40 feet high.

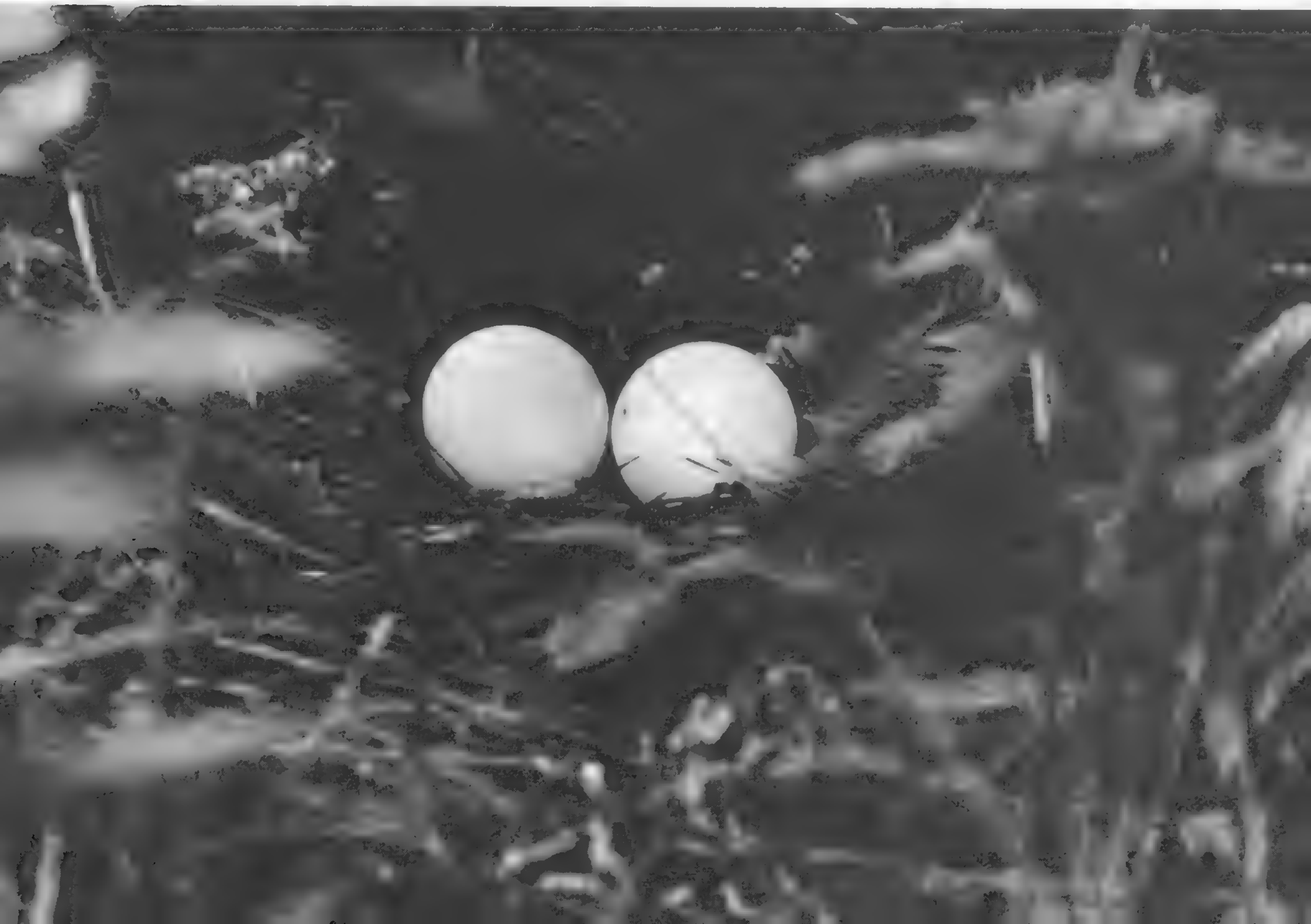
Mr. Harmon had been aware of the presence of these owls during the previous summer and fall. He had heard them from his farm home, only 500 yards from the woods, and had, on several occasions, seen them swoop down at dusk in pursuit of the cotton rats that persisted about his outbuildings. The nest in the woods was 400 feet from the nearest open lot and only 200 feet from a dirt road used regularly by the local farmers.

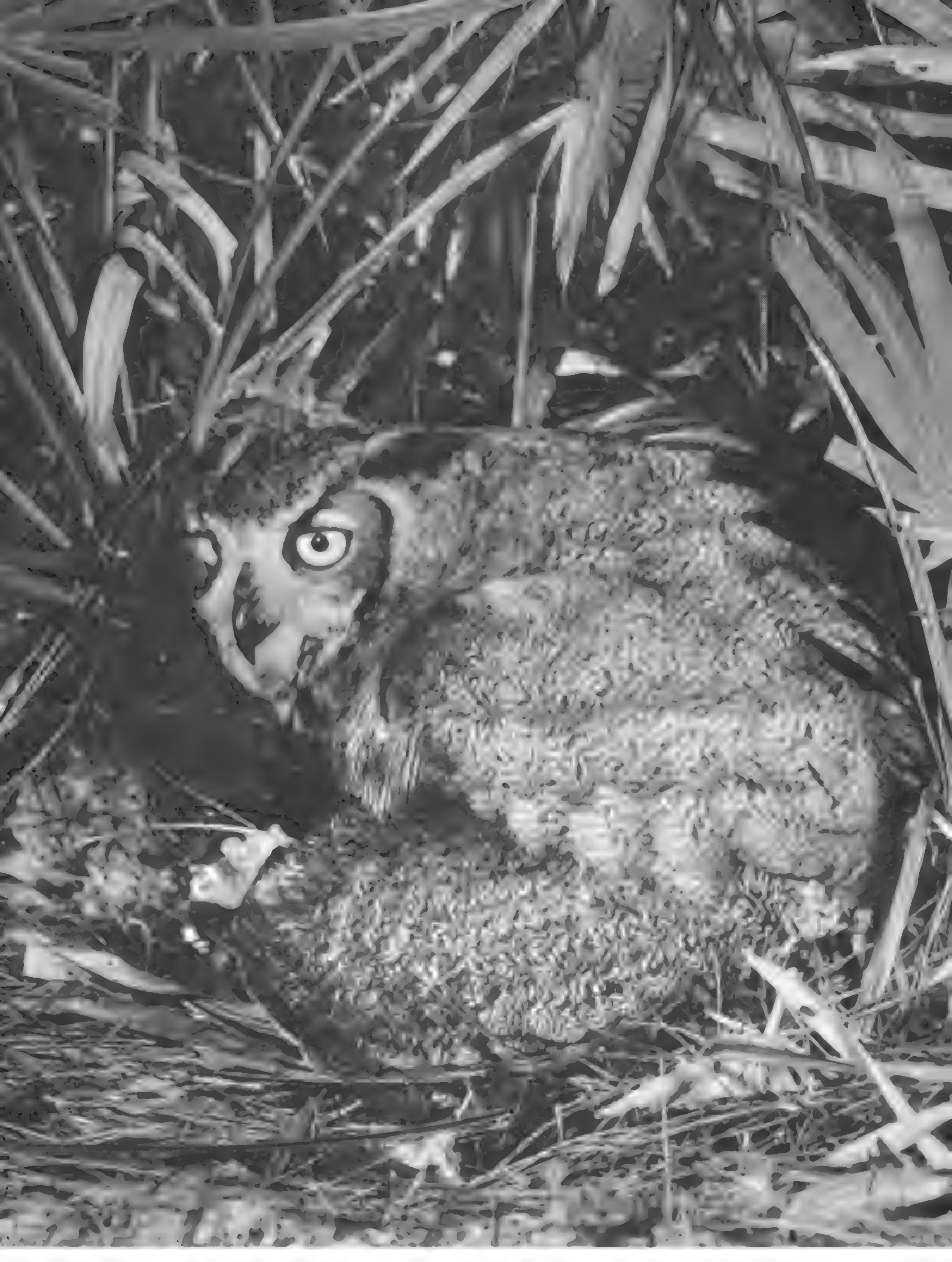
After finding the nest, Mr. Harmon visited it about twice a day until the eggs hatched on 19 January 1965 (29 days after the nest was found)—one the previous night, the other in the early afternoon. I first saw the nest on 6 January and set up a blind on 21 January. From 25 January, when I took my first pictures, until 22 February, when I could no longer find the young in the woods, I photographed the owls from the blind almost every night. Since there was almost no activity at the nest until about sundown, I entered the blind about 4:15 PM and left it between 9:30 PM and 12:30 AM. During this same period the quail-hunting season was on in Florida. I therefore spent many daylight hours in the blind or in the woods, watching and trying to keep the hunters from destroying the nest or shooting the adults that were always nearby.

Each adult Great Horned Owl had its own two or three favorite perches. According to my observations, one bird stayed on a perch about 50 yards away and never came to the nest; the other stayed on the nest almost all the time during incubation and the first week of brooding. Later, after the young were eight or nine days old, it sat on a perch about 20 feet above them. I never saw two adults at the nest at the same time. It is my impression, from what I saw of the nest and perches, that it was always the same bird that incubated the eggs and brooded and fed the young. Although I have no proof, I presume that this bird was the female and shall refer to it as such.

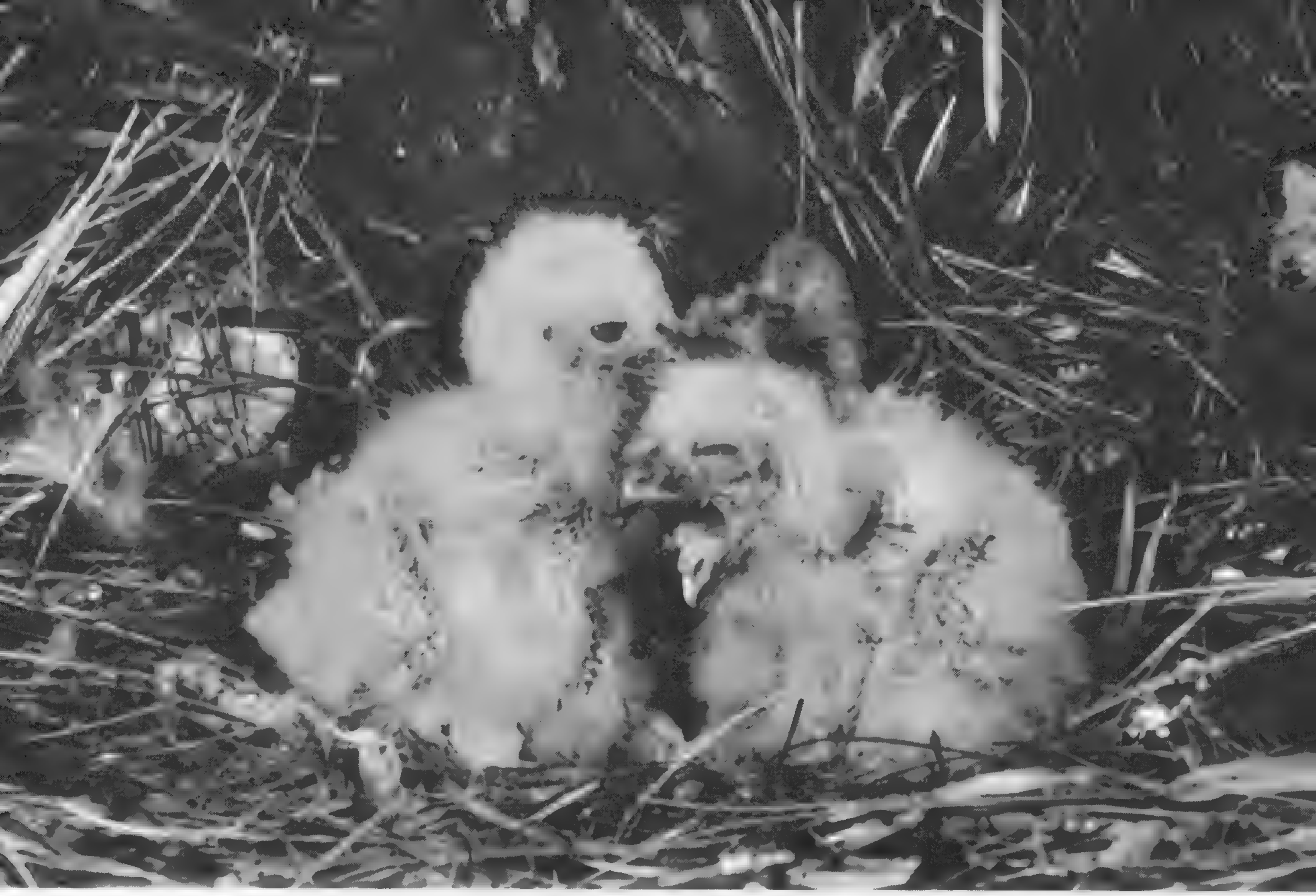
During the period of incubation we visited the nest only in daylight. The female always left the nest when an intruder was from 35 to 150 feet away, and neither bird made any attempt to attack. As the intruder withdrew, the

Above, the blind. The nest of the Great Horned Owl is about 20 feet away, on the ground under a 3-foot palmetto bush. When the young were two days old, 21 January 1965, I set up the blind on a 5-foot tower and each day for the next three days moved it closer to the nest until it was 19 feet away. *Below,* the nest. (Photograph by Robert Haugen, National Park Service.) The two white eggs rested on a layer of pine needles which, though no thicker than the carpet around them, were twisted in a somewhat circular fashion — probably by the turning of the bird's body. There was no other nesting material.

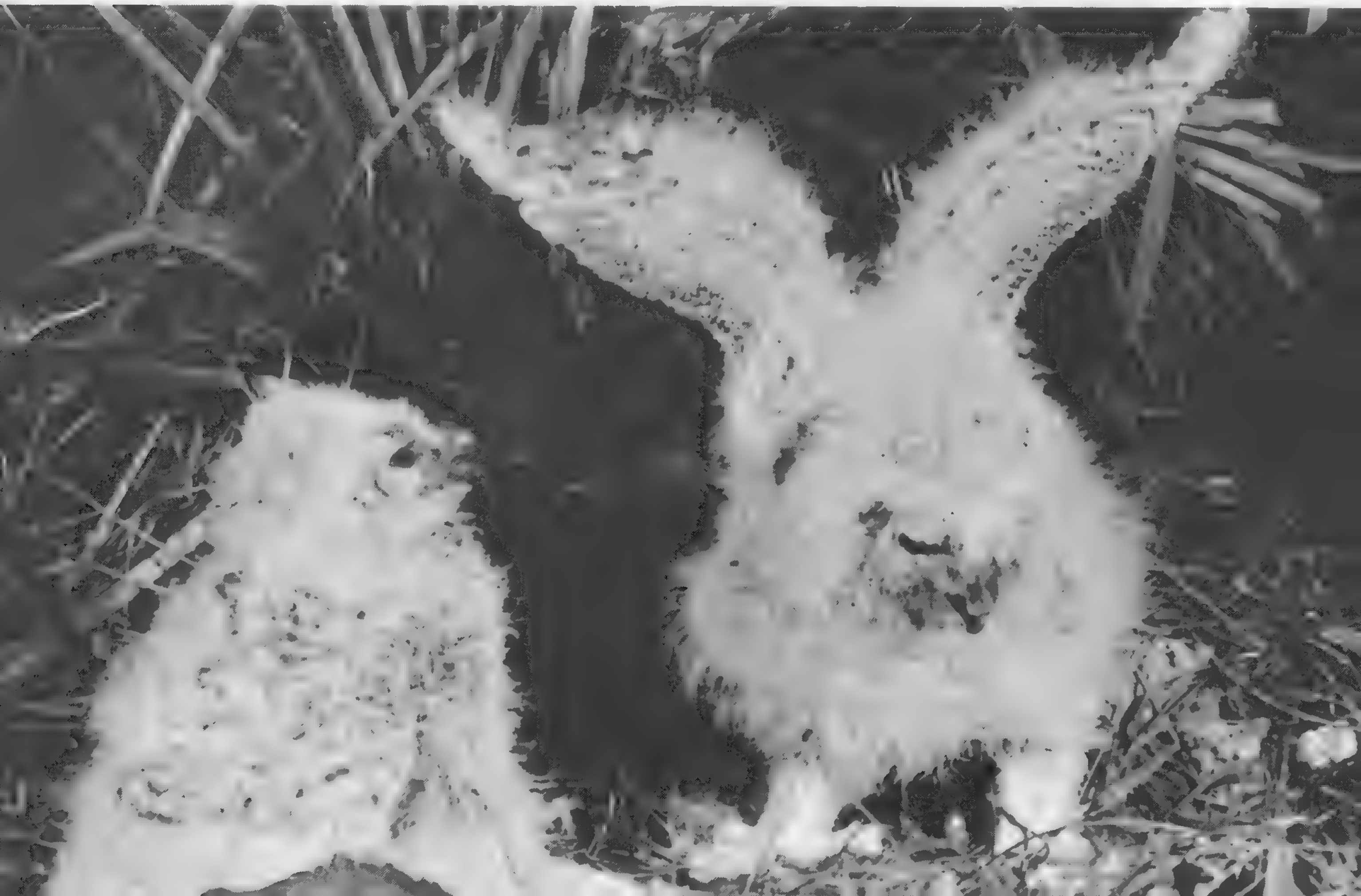


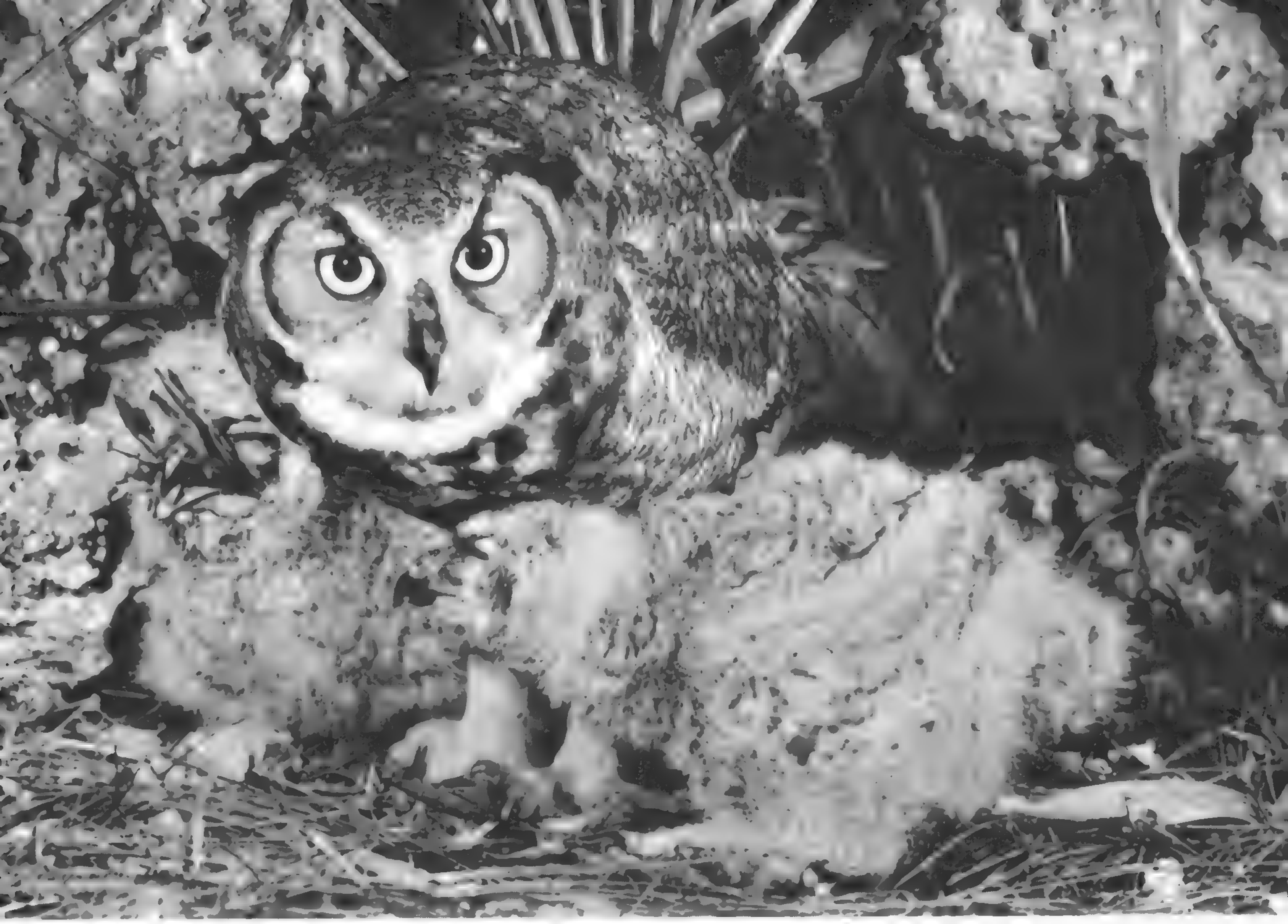


The female Great Horned Owl about to feed the 6-day-old young, 25 January 1965. Until the young were about 8 or 9 days old, the female covered them even while feeding. The first feeding of the day took place just after sundown. The male came to the tree above carrying a freshly killed bird or rat; the female flew up, took the food, and returned to the nest. She fed the young the soft inside parts and strips of meat less than an inch long. By turning her head sideways she allowed the young bird to insert its open bill into hers — on either side of the meat — and take the meat from her bill.

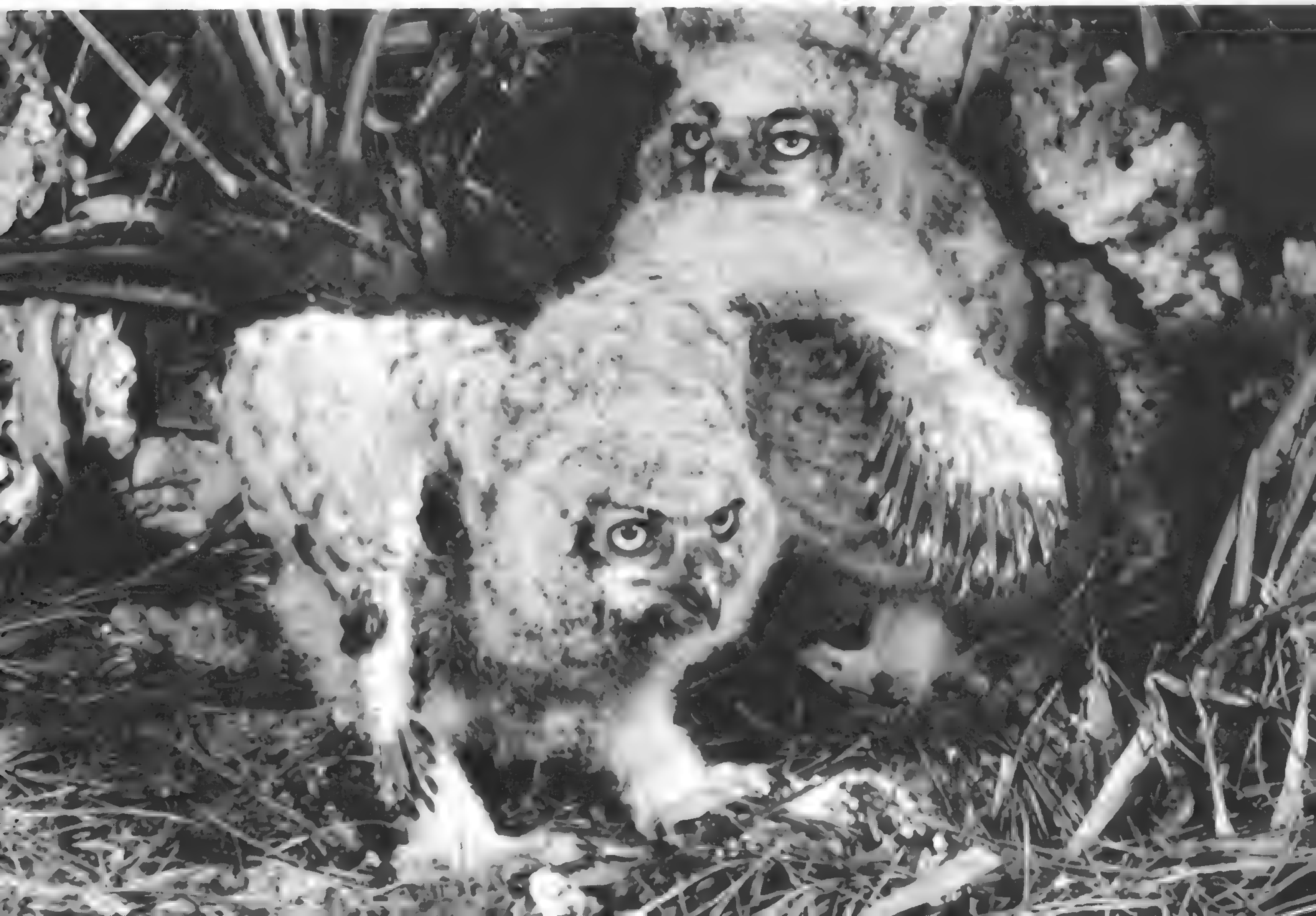


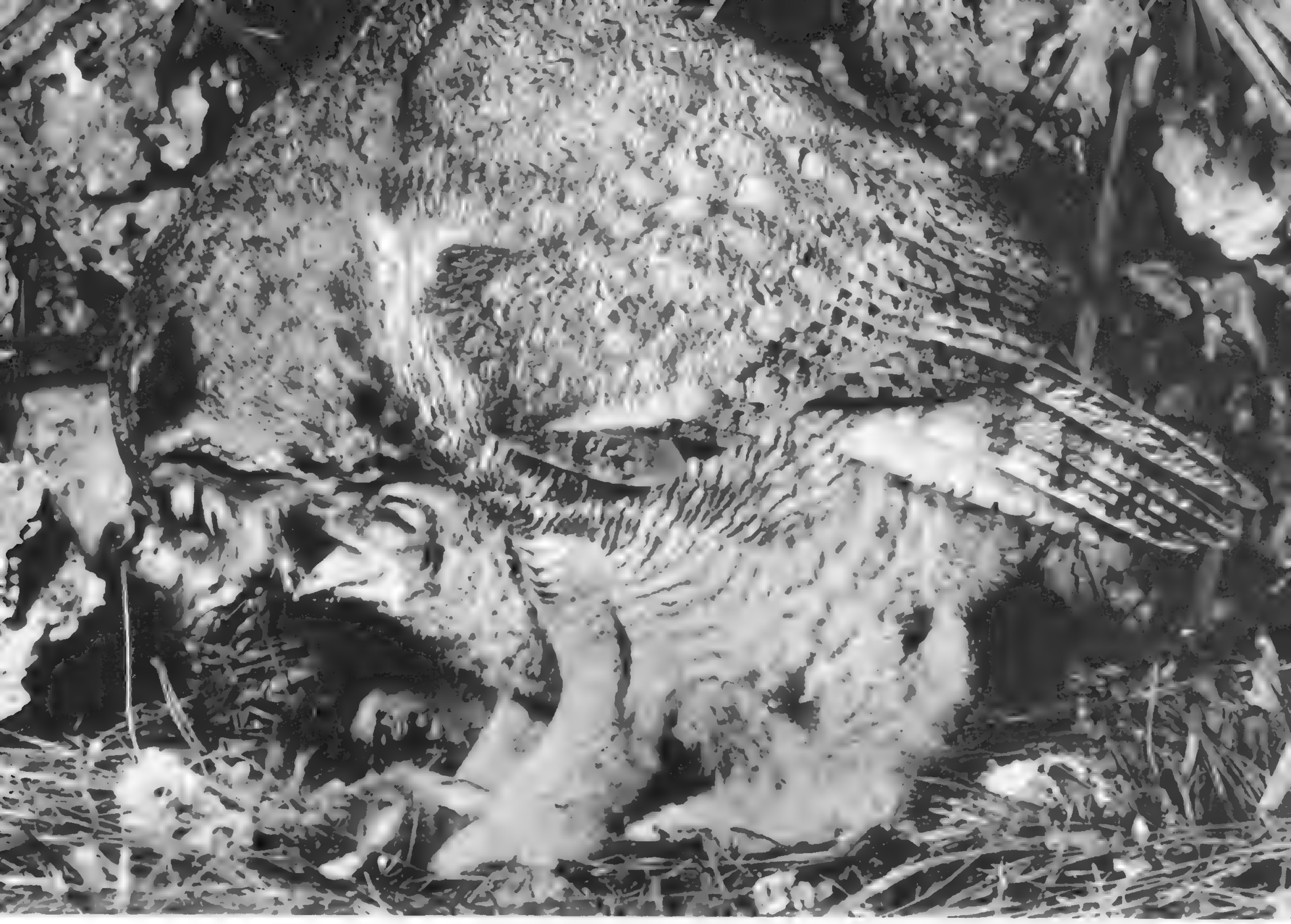
Above, young Great Horned Owls, 10 days old, 29 January 1965. At this stage the female ceased brooding the young in the daytime, even in light rain, and sat on a pine limb about 20 feet above the nest. She slept, preened, or just gazed down at them for long periods, uttering low "mewing" sounds. Very infrequently she flew down, walked around the nest, touched the young with her bill, and flew back to her perch. *Below,* the young, 16 days old, 4 February. I never saw the female feed the young in daylight, and, although they sometimes pecked at a bird or a rat when the female brought it, I never saw the young feed themselves at any time. Hoping to get a picture of feeding in daylight, I placed a freshly killed Catbird in the nest that morning about 9:30. The female sat on the branch above and made no move to feed it to them until dark. The young ignored it. In fact one young *(left),* the second in the peck order, sat on the bird all day.



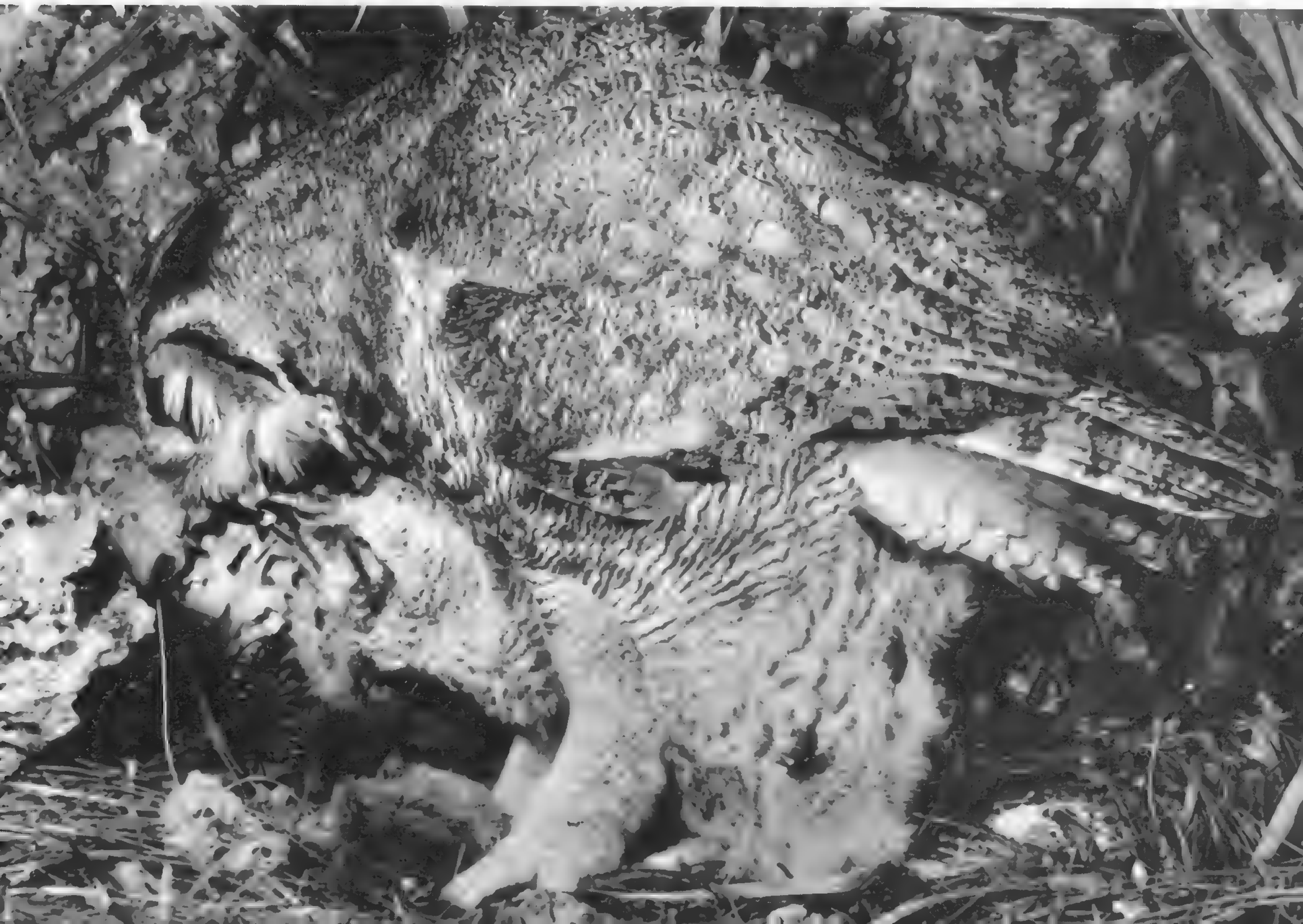


Above, the female and young, 21 days old, 9 February. A large portion of a Robin, feathers and all, is just disappearing down the throat of one young; the other looks interested. The food consisted chiefly of Robins and cotton rats in equal numbers together with a few Catbirds, Brown Thrashers, Yellow-shafted Flickers, and smaller birds that I could not identify. *Below,* the young, 23 days old, 11 February. They exercise while waiting for another feeding. Note that the nest is quite clean and that there is no accumulation of leftover bits and pieces. The young ate what the female brought and I never saw her eat anything at the nest except some portions that they refused.

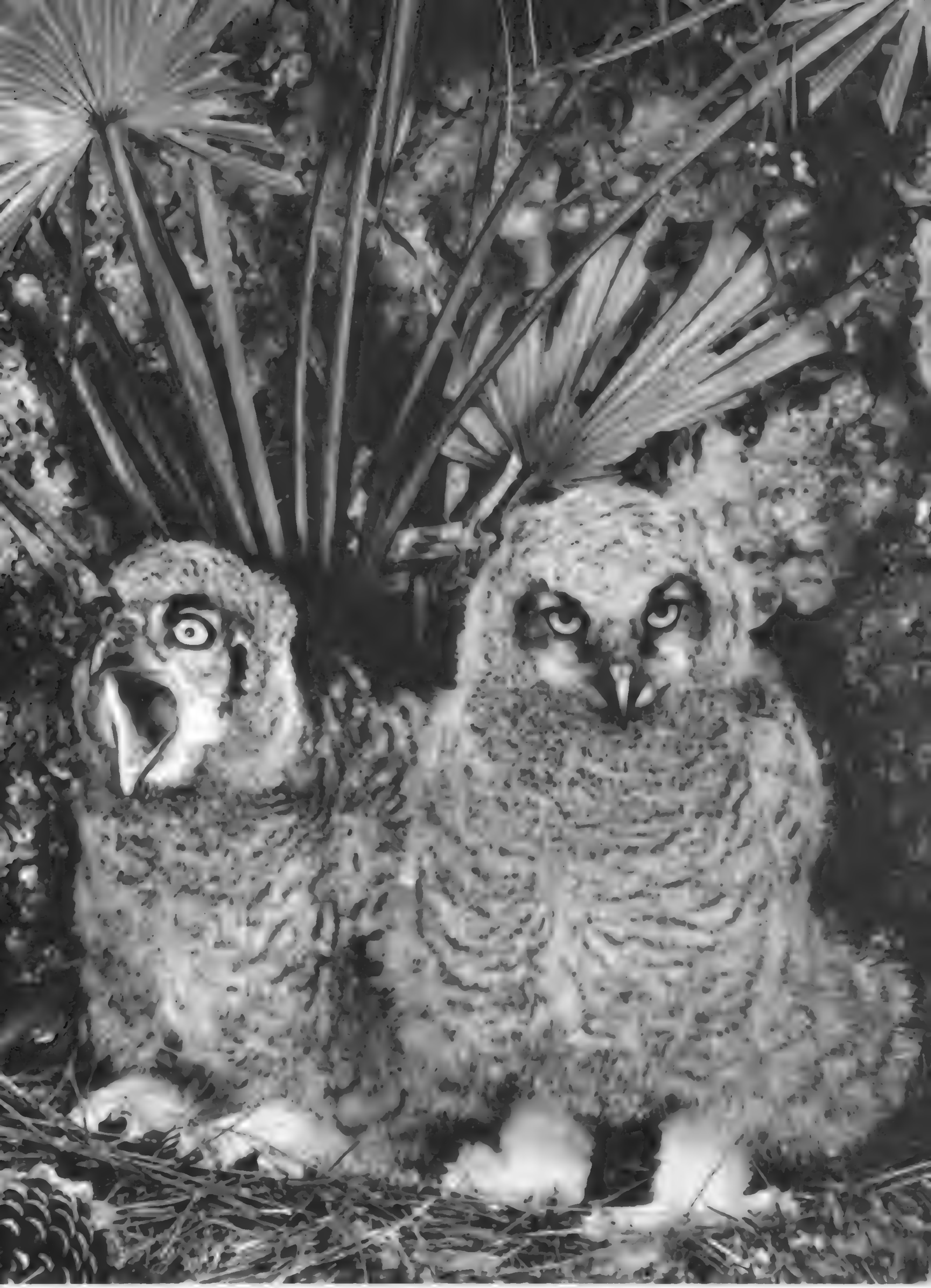




Above, below, and *opposite,* female Great Horned Owl with young, 23 days old, 11 February 1965. As the young grew older, the method of feeding became faster and the portions larger. By the time the little owls were 20 days old, the female fed them only two or three times each night during my observations and the procedure was increasingly violent. For example, she would come with a Robin, rip off a wing, and shove it down the young bird's throat, or, as in these four pictures, she might bring a rat, tear off a hind quarter, and push it into the upraised bill with a fierce "take it and like it" approach. I have worked with a number of



other birds of prey — Goshawks, Red-tailed and Red-shouldered Hawks, Golden and Bald Eagles, Ospreys, Barred Owls among them— and I have watched their feeding from hatching to flight. I have seen them devouring all kinds of food. For example, I have watched young Red-shouldered Hawks pick up and swallow whole frogs and snakes and young Red-tailed Hawks feed themselves on naked baby songbirds, but I have never, in my experience, seen any bird feed young as roughly as did this Great Horned Owl after the young were 20 days old.



Young Great Horned Owls, 28 days old, 16 February 1965, about 7:30 PM, following their second feeding. After this picture was taken, the two young birds ran from the nest for the first time. I found them the following morning — one about 300 yards south of the nest, the other about 400 yards west. I returned them to the nest where they stayed until evening.

Above, the young, 29 days old, 17 February. The two young having been well fed are about to set off on their own. After this they ran from the nest more frequently and with the help of a hunting dog I found them each morning and brought them back. While I searched for them and carried them back to the nest, the female followed me from tree to tree but never showed any sign of aggressive behavior. *Below,* the young, 32 days old, 20 February. They take a look at the light before leaving for the night. I found them the next morning for the last time. Although I failed to locate them thereafter, I believe, from the behavior of the adults, that they were still in the woods.

female followed him, flying from tree to tree about 20 feet above his head until he reached the road. Then she returned to the vicinity of the nest and within five or ten minutes was back on the eggs. After the young hatched and until they were eight or nine days old, she covered them all the time, even while feeding them.

The female paid scant attention to me in my blind. She did not even mind my focusing light if I turned it on while she was on the nest. However, she would not return to the nest if the light was on. To solve the problem of knowing—in the darkness—whether or not she was on the nest, I placed dry palmetto fronds in her entrance path. About two seconds after I heard the fronds rustle, I could turn on the light without disturbing her.

After the young hatched, I went to the blind each night. Once, and only once, did I approach the nest intending to adjust the strobe lights. The female flushed and, as I drew close to the nest, one of the owls swooped down and clipped me hard on the back of the head. After that I went directly from the road to the blind and stayed there. Although she never seemed disturbed after I entered the blind, she escorted me to and from the blind on each nightly visit for over four weeks.

All during the time I photographed these owls they never became any tamer than on the first day. The female never allowed me to come closer than 35 feet without flushing; and she continued to refuse to return to the nest when the focusing light was on. This behavior was quite in contrast to that of a Barred Owl whose nest I photographed on the ground in the Everglades. The Barred Owl became so used to me that I could lift her off the nest to inspect the eggs without any display of defensive behavior on her part. She became aggressive only after her daylight brooding which ceased at the end of two weeks.

It may be of interest to note the size of the pupil in the eye of the adult in the photographs on pages 179, 181, and 183. The amount of light (two strobe heads at four feet) projected straight in the eye of the bird was the same in all cases as was the distance of the light from the bird, yet the size of the pupil is smaller in the photograph on page 179, taken 25 January, than in the other photographs taken on 9 and 11 February. These pictures may give substance to the idea that emotion as well as light controls the pupil in the eye of the owl. And if more intense emotion, in this case fear, means a closing of the pupil, these pictures may indicate that, despite her continued wildness, the Great Horned Owl did slightly adjust to the continued presence of the photographer in his blind.

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THE ROLE OF MIGRANT BIRDS AT SWARMS OF ARMY ANTS

Edwin O. Willis

The migration of birds has interested ornithologists for years. There have been dozens of studies of how birds orient or navigate, how weather and photoperiodism affect timing and preparation for migration, and where and when birds migrate. A remarkably unexplored field is the ecology of migrant birds. How do migrant birds exploit food in areas, especially tropical ones, which already seem saturated with resident species?

Skutch (1950) and Moreau (1950), in discussing breeding seasons of tropical birds, suggest that migrant birds are less important than are other environmental factors in determining breeding seasons. Moreau (1952), in a general summary of observations of palaearctic migrants in Africa, notes that some migrants wander widely, others share possibly superabundant food with allied resident species, and that these and other adjustments between migrants and residents are worth detailed study. Morel and Bourliere (1962), in an important and detailed study of migrant and resident birds on a savanna in Senegal, conclude that migrants constitute a "floating population" of consumers using foods which cannot be exploited by resident species. Slud (1960) suggests that migrant birds in a wet lowland forest in Costa Rica generally complement native species ecologically rather than compete with them. In contrast to the preceding workers, Miller (1963) suggests that, in a highland cloud forest in equatorial Colombia, migrants may outcompete residents to the extent of limiting their reproduction from October to February. Few other authors have even speculated whether migrant and resident birds influence each other ecologically.

During studies of birds which follow army ants in various lowland forests in Central and South America, I occasionally found migrant and wintering species with the resident birds. The ant-following birds congregate over swarms of a few army ant species, mainly *Eciton burchelli* and *Labidus praedator*; there they snap up insects and other arthropods flushed by the ants (Johnson, 1954). It is easy to observe the frequent supplantings and foraging activity of birds over the swarms of ants, since the birds are crowded into a small space in the forest undergrowth. This paper will consider how the migratory birds fit into these highly competitive groups of birds over the swarms of army ants.

Study Areas and Methods

I obtained most of my observations during an intensive study of ant-following birds on Barro Colorado Island between 30 September 1960 and

TABLE 1

Important Areas Where Birds Were Studied at Swarms of Army Ants

Locality	*Elevation in meters*	*Rainfall in meters per year*	*Dry seasons*	*Time visited by author*
British Honduras				
Gallon Jug (17° 33′ N Lat., 89° 01′ W Long.)	100	1.7	January–April	13 February–2 August 1957
Costa Rica				
Golfito (8° 38′ N Lat., 83° 10′ W Long.)	300	4.5	December–March	25–28 March 1961
Panama (Canal Zone)				
Barro Colorado (9° 10′ N Lat., 79° 51′ W Long.)	25–165	2.7	December–April	See text
Buenavista Point (9° 11′ N Lat., 79° 50′ W Long.)	25–50	2.7	December–April	23 October 1960
Bohio Peninsula (9° 12′ N Lat., 79° 51′ W Long.)	25–100	3	December–April	21 January, 4–7 February 1962
Forest Reserve (9° 06′ N Lat., 79° 37′ S Long.)	200	2.5	December–April	27–29 September, 2, 9 November 1961
Río Agua Salud (9° 12′ N Lat., 79° 48′ W Long.)	25–100	3	December–April	10 February 1965
Colombia				
San Pedro (8° 27′ N Lat., 76° 18′ W Long.)	150	2.5	December–April	11–16 March 1965
Remedios (7° 02′ N Lat., 74° 41′ W Long.)	800	2.7	December–April	1–14 May 1962
El Tigre (4° 57′ N Lat., 76° 30′ W Long.)	80–400	6	(February)	26 February–7 March 1962
Tres Esquinas (0° 44′ N Lat., 75° 15′ W Long.)	200	3	February–April, September–October	10–22 April 1962
Trinidad				
Simla (10° 42′ N Lat., 61° 17′ W Long.)	300	2.7	December–April	26 November–19 December 1961
British Guiana				
Nappi Creek (3° 17′ N Lat., 59° 30′ W Long.)	200	2.5	February–April, September–October	24 December–5 January 1962

25 November 1961. Some additional information on wintering birds came from my visits to the island from 18 January to 18 February in 1962 and 16 January to 4 March 1965. Other localities where I watched migratory species at or away from swarms are listed in Table 1.

Ecological Conditions

The forests and conditions of observation were fairly similar at all locations. All are lowland forests, hot and humid, with a dense upper canopy and relatively open undergrowth in which buttressed trunks and slender saplings rise vertically from a thin layer of recently fallen leaves. Here and there a fallen tree has created a gap in the canopy, marked near the ground by a tangle of branches and vines around the trunk. Later rank shrubs and saplings crowd around the decaying log and create a patch of dense undergrowth. Slender saplings, decaying logs, and low places in the canopy mark old treefalls. On Barro Colorado, patches of wild pineapple (*Ananas magdalenae*), a spiny-leaved bromeliad, also interrupt the open undergrowth. In all areas, treefalls and patches of clear or dense undergrowth form a mosaic of habitats in the shade of the forest.

On Barro Colorado, which is an island in Gatun Lake formed by flooding the lowlands for the Panama Canal, the youngest forests are over 40 years old and hard to distinguish from old growth. In other areas that I visited, the mature forests are broken by clearings and dense second growth of various ages. It was so difficult to observe birds in this very dense second growth that I generally worked in tall forests such as on Barro Colorado.

Most of the areas where I worked had high rainfall, with one or two rainy seasons per year (Table 1). Where rainfall is above three meters a year, such monocotyledonous plants as aroids, philodendrons, and gingers tend to crowd the undergrowth and cover the trunks of trees. Forests in areas with less than two meters of rainfall tend to be 20 to 30 meters tall, as is old second growth on Barro Colorado, rather than 25 to 40 meters tall as in areas with more than two meters of rainfall annually. The habitats and climates of several of my study areas have already been discussed more fully by other writers (see Kaufmann, 1962, for Barro Colorado; West, 1957, for El Tigre; Snow, 1962, for Simla).

The Army Ants

The army ants *Eciton burchelli* and *Labidus praedator* form broad swarms of thousands of individuals in tropical forests from Mexico to Argentina (Rettenmeyer, 1963). Both species catch and tear apart many species of arthropods; they bite and sting birds encountered but, contrary to common belief, do not tear apart vertebrate flesh. Arthropods and small vertebrates fleeing the gradual advance of a swarm are ready prey for parasitic flies and ant-following birds.

Eciton burchelli, a large ant which flushes mostly cockroaches, spiders, and similar large prey, swarms along the ground, 15 meters or so per hour and 100 to 200 meters per day, and sends occasional probes up tree trunks and into elevated tangles during its raids. Although it swarms all year, each colony becomes relatively inactive during a space of two weeks every five weeks. Each period of inactivity falls in the middle of a "statary period," — i.e., a space of three weeks when the colony stays in the same spot and any raids radiate out like the spokes of a wheel on successive days. Alternating with statary periods are "nomadic periods" of about two weeks each when the ants change the site of their nest or bivouac nearly every night. Schneirla (1957) showed that these nomadic-statary cycles are caused by reproductive cycles and continue all year; larvae are present during each nomadic phase, eggs and pupae during each statary phase.

Labidus praedator is a small black ant which, when it swarms, rarely ascends more than two or three meters up tree trunks or bushes. It flushes many sowbugs and other small prey, but it too scares up some large arthropods like those flushed by *burchelli*. It swarms over a more or less regular serpentine or spiral course in a small area rather than marching steadily ahead. It moves at any hour of day or night. After a few hours of swarming it is likely to disappear underground. During dry weather it rarely swarms above ground, but in rainy weather it swarms on the surface rather commonly. Since it swarms irregularly and unpredictably, resident birds follow its swarms much less than they do the regular swarms of colonies of *burchelli*. (For detailed accounts of the swarming and other behavior of *Labidus praedator* and *Eciton burchelli*, see Rettenmeyer, 1963).

Methods of Study

To observe birds at swarms of army ants, I stood 10 to 20 meters behind swarms and stayed as still as possible until birds had returned and showed little mobbing, fear, or other disturbed behavior. The heights, perch angles, and perch diameters of birds waiting for prey I estimated at irregular intervals in such a way that no two observations represent the same bird on the same perch. For instance, the notation "K 03/15 y 2" in my notes means that a foraging Kentucky Warbler (*Oporornis formosus*) stood on a perch that was between 0.2 and 0.3 meter above the ground, had an angle of 10 to 15 degrees from the horizontal, and was between one and two centimeters in diameter.

For foraging motions, I noted whether the bird was flying ("sallying") or perched ("lunging") when it attacked the prey; and I recorded perching birds that were tossing leaves or digging in a log or tree trunk. The location of the prey during attempts at capture I recorded as the air, ground, leaf, twig, stem, trunk, vine, or the like as specifically as possible. I have often grouped the specific locations, as liana with stem or petiole with leaf, whenever there were few observations for a location. I found it impossible to estimate success of prey capture, since I could rarely tell whether a bird had missed the prey or had swallowed the small prey so quickly that I overlooked it.

In this paper I use "supplanting" to mean overt chases. "Displacings" are cases when a bird retreated as another bird came by.

During the course of this paper I shall mention repeatedly 11 species of tropical birds:

Great Rufous Motmot, *Baryphthengus ruficapillus*

Squirrel Cuckoo, *Piaya cayana*

Plain-brown Woodcreeper, *Dendrocincla fuliginosa*

Buff-throated Woodcreeper, *Xiphorhynchus guttatus*

Slaty Antshrike, *Thamnophilus punctatus*

Spotted Antbird, *Hylophylax naevioides*

Bicolored Antbird, *Gymnopithys (rufigula) bicolor*

Ocellated Antthrush, *Phaenostictus mcleannani*

Bright-rumped Attila, *Attila spadiceus*

White-throated Robin, *Turdus assimilis*

Gray-headed Tanager, *Eucometis penicillata*

Unless otherwise noted, all my observations listed in tables refer to birds at swarms of army ants on Barro Colorado. Estimates of such measurements as perch height I have listed under the upper limit for each group. For example, 50 records at 0.1 meter mean that the species on 50 occasions stood on perches between the ground and 0.1 meter.

In all study areas I wandered many hours through the forests at an average rate of about two kilometers per hour, looking for ants and censusing or observing birds. On Barro Colorado I spent nearly as many hours censusing away from swarms as I did watching at swarms; excluding observations in 1965, I spent 1,845 versus 2,017 hours, respectively. In addition, I made some observations during rains when hurrying, when watching the behavior of species away from swarms, or under other conditions so unfavorable for systematic censusing that I did not list the hours. In other areas the ratio of hours I spent censusing, or simply observing apart from swarms, to hours watching at swarms was higher, perhaps 1.5 to 1. At the end of each day I recorded in my field notebooks the total number of individuals of each species at or away from swarms and during or outside of censusing hours. These estimates are generally minimal ones, as birds encountered away from swarms are likely to be forgotten at the end of the day, especially when a species is common. However, my totals give some indication of the relative abundance of a species from month to month and year to year. The numbers are also useful in discussing what proportion of the individuals use swarms, as long as one remembers that a casual censusing method paired with intensive watching at swarms will tend to overestimate the proportion following ants. Table 2 lists the total numbers for seven migrant species which commonly follow swarms on Barro Colorado.

Species Accounts

Tyrannidae

Resident species of tyrant flycatchers seldom follow ants, since the ants rarely move into open areas or into the canopy where most flycatchers work. Moreover, the ants flush rather few flying prey. Migrant flycatchers, excepting Acadian Flycatchers, seldom visit swarms.

Great Crested Flycatcher (*Myiarchus crinitus*).—One individual of two wandering about a partly burned clearing in the dry forests at San Pedro, Colombia, on 12 March 1965 dropped to attend a weak swarm of *Eciton burchelli* and captured two insects before flying on. The resident ant-following birds had deserted this swarm as soon as it moved into the clearing, although one Plain-brown Woodcreeper visited nearby stubs periodically. The woodcreeper flycatches actively and normally catches any arthropods large enough to attract the flycatcher. None of the 45 other Great Crested Flycatchers observed at San Pedro during a period of five days visited any other swarms I watched.

TABLE 2

Numbers of Seven Migratory Ant-Followers on Barro Colorado

Month	*Total days of observations*	*Acadian Flycatcher*	*Wood Thrush*	*Swainson's Thrush*	*Gray-cheeked Thrush*	*Veery*	*Kentucky Warbler*	*Canada Warbler*
1960								
October	28[1]	196	10	231	122	22	106	128
November	27	235	99	232	104	18	126	4
December	28	111	55	8	3		70	
1961								
January	28	132	62	1	1		52	
February	20	111	35		1		36	
March	23	111	30	2			43	
April	28	47	3	36	1		3	37
May	28	1		2				4
September	25	14		1		2	5	12
October	30	213	19	56	59	4	103	82
November	22	118	49	14	20		42	6
1962								
January	13	41	9				24	
February	14	29	2				9	
1965								
January	15	58	8				59	
February	25	47	17	1			46	

[1] Number of days of observation during month.

On Barro Colorado, as many as eight Great Crested Flycatchers have been recorded per day in October and March. Between these months the species is less common, with about four per day. I recorded one bird as early as 20 September 1961 and another as late as 25 May 1961; the latter bird called in the same area for several weeks before its unusually late departure. The species calls *whooip* loudly and persistently from inside the crowns of forest trees, where it sallies to capture prey on vegetation and in the air. Such persistent calling by widely scattered wintering and migrant birds of this and other species may indicate that they are maintaining intraspecific territories with call notes, as Schwartz (1964) found for Northern Waterthrushes in Venezuela.

Once, when a Great Crested Flycatcher came near an active swarm on Barro Colorado, it ignored the ants. This species probably visits swarms only under unusual conditions. The widespread members of the resident woodcreeper genus *Dendrocincla* seem to occupy the niche that the flycatcher could take if it moved near the ground.

Eastern Wood Pewee (*Contopus virens*).—One bird waited and hawked for several minutes over a swarm of *Labidus praedator* in a large treefall on Barro Colorado, 7 December 1960. A second pewee, perched above a swarm of *Eciton burchelli* at the edge of a treefall clearing, twice sallied to catch prey dropping from near a probe of ants moving up a dead tree, 21 October 1961. A third bird waited four meters up at the edge of a large treefall clearing on 25 October 1961, then darted down to an approaching swarm of *burchelli* and snapped up one tiny insect. Several other birds, waiting on or near treefalls or dead trees, ignored passing swarms, even when resident birds were actively capturing prey.

I found the Eastern Wood Pewee a common migrant on Barro Colorado as early as 30 August 1961 and as late as 14 December 1960, with peak numbers of 10 to 20 birds per day in mid-October. The species was less common between 11 March and 21 May 1961, with peak numbers of eight birds per day about 20 April. In fall, scattered and perhaps territorial birds persistently whistle *peereet,* a gliding whistle rather like one song used on the breeding grounds. In spring they call less often. There may have been a few Western Wood Pewees (*Contopus sordidulus*) among the above birds, but I have not heard its distinctive calls or seen a dark-breasted bird definitely like it anywhere in lowland tropical forests.

Most pewees stay atop dead forest trees or at the edges of openings in the forest. They sally into the open air more frequently than they dart into the shade, foraging in much the same way as they do on the breeding grounds. They visit the forest interior less frequently than on the breeding grounds. The pewee's niche, occupied by no native species, includes swarm-following only under unusual conditions.

Traill's Flycatcher (*Empidonax traillii*).—Two birds, one singing the "way-bee-o" song and both giving the "wit" call note typical of this species, worked from two to four meters above a swarm of *Eciton burchelli* in a bushy gully in a pasture at Tres Esquinas, Colombia, between 8:00 and 10:00 AM on 11 April 1962. They sallied short distances to the foliage for tiny prey. The ants, on the ground most of the time, probably flushed few items taken. A pair of wrens (*Thryothorus coraya*), pecking at twigs and stems nearby, ignored the flycatchers. Infrequently, when swarms of ants visit bushy pastures, the Traill's Flycatcher may fill the same role as does the Acadian Flycatcher.

Acadian Flycatcher (*Empidonax virescens*).—I observed some 157 individuals, probably of this species (see comments on identification under the next species, the Yellow-bellied Flycatcher), at 132 swarms on Barro Colorado (Table 3). They attend swarms most commonly in October and November; except for a minor resurgence in March and April, there are few records of swarm-following during other months.

On Barro Colorado the species was recorded from 6 September 1960 to 1 May 1961: as many as 15 or 20 per day in late October and early November; up to 10 per day in March; and an average of five per day in between (Table 2).

Away from swarms this flycatcher occupies the zones of moderately thick foliage from one to 15 meters above the ground, keeping in the shade and well below the canopy much of the time. Although this species occasionally forages out over a treefall or clearing, it rarely captures prey in direct sunlight. At swarms it often forages closer to the ground (Table 4). For the most part it sallies for short distances to leaves, small twigs, or into the air (Table 5). The small insects or berries taken are generally swallowed instantly. Sometimes prey, up to half again as long as the bill, is shaken and chewed, but I have never seen the bird use the perch as an anvil. The stomach contents of four specimens, taken above swarms on Barro Colorado, included ridged seeds of melastome berries, roaches, a chalcoid hymenopteran, wings of bugs and beetles, a termite, and a sowbug; the stomach contents of a bird from the Forest Reserve included a sowbug, a spider, two bugs, a beetle, and a melastome berry. The contents of all five of the stomachs were mostly fragments of unidentifiable insects.

As this flycatcher looks about from slender, horizontal twigs, it often twitches the tail or calls *wreep* loudly, a note that may be a territorial call. Although I heard song only a few times, I surmised that individual flycatchers were rather widely spaced throughout the forest undergrowth on Barro Colorado, and hence may hold winter territories.

No more than two Acadian Flycatchers attended any one swarm of ants before December and no more than one after December. On a few occasions in October two birds ignored each other; on other occasions one chased the other off with bill-snapping and sputtering calls, such as *wreer titit, peet, pee-eet,* and *chibit.* Once the perched attacker fluttered its wings and spread its tail before flying at the other. I recorded 11 intraspecific supplantings at swarms of army ants.

Interspecific supplantings were rare: a Great Rufous Motmot, a Plain-brown Woodcreeper, a Bicolored Antbird, a Bright-rumped Attila, a Spotted

TABLE 3

Swarm Attendance by Acadian Flycatchers on Barro Colorado

	Ant species					
	Eciton burchelli			*Labidus praedator*		
Month	*Swarms*	*Number of swarms*	*Number of Fly-catchers*	*Swarms*	*Number of swarms*	*Number of Fly-catchers*
1960						
October	30[1]	5 (17%)[2]	6[3]	43	6 (14%)	8
November	24	11 (46)	12	37	29 (78)	41
December	31	11 (35)	13	25	3 (8)	3
1961						
January	40	1 (2)	1	12	4 (33)	4
February	43	2 (5)	2	14	1 (7)	1
March	42	6 (12)	6	7	1 (14)	1
April	59	6 (10)	6	8		
May	58[4]			6	1	1
September	69			11		
October	78	20 (26)	23	18	9 (50)	12
November	51	9 (18)	10	7	2 (28)	2
1962						
January	29	1 (3)	1	14		
February	24			3		
1965						
January	26			10		
February	69	3 (4)	3	9	1 (11)	1
Totals	673	75	83	224	57	74

[1] Number of active swarms watched more than 5 minutes each.

[2] Total number and per cent of swarms attended by flycatcher.

[3] Total number of flycatchers at swarms.

[4] 1 to 20 May only.

TABLE 4

Heights of Perches and Attempts at Prey for Acadian Flycatchers

	Height in meters										
	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*
Number of perches	37	88	73	41	25	13	11	3	7	2	
Number of prey	30	56	56	20	14	5	3	1		2	1

Antbird, and a Gray-headed Tanager each supplanted the Acadian Flycatcher once.

The Acadian Flycatcher seldom foraged like any species of resident bird except the inoffensive Red-capped Manakin (*Pipra mentalis*), which sallies to the foliage for small prey and berries in about the same way. Like the flycatcher, the manakin follows swarms mainly in October and November when young of the year and swarms of *Labidus praedator* are both numerous. However, the manakin depends on fruit to a much greater extent. It also tends to wait on bare branches towards the centers of saplings and sally long distances to the terminal twigs rather than sit in the terminal twigs and sally short distances as does the flycatcher. Unlike the flycatcher, the manakin captures more prey on the foliage than in the air.

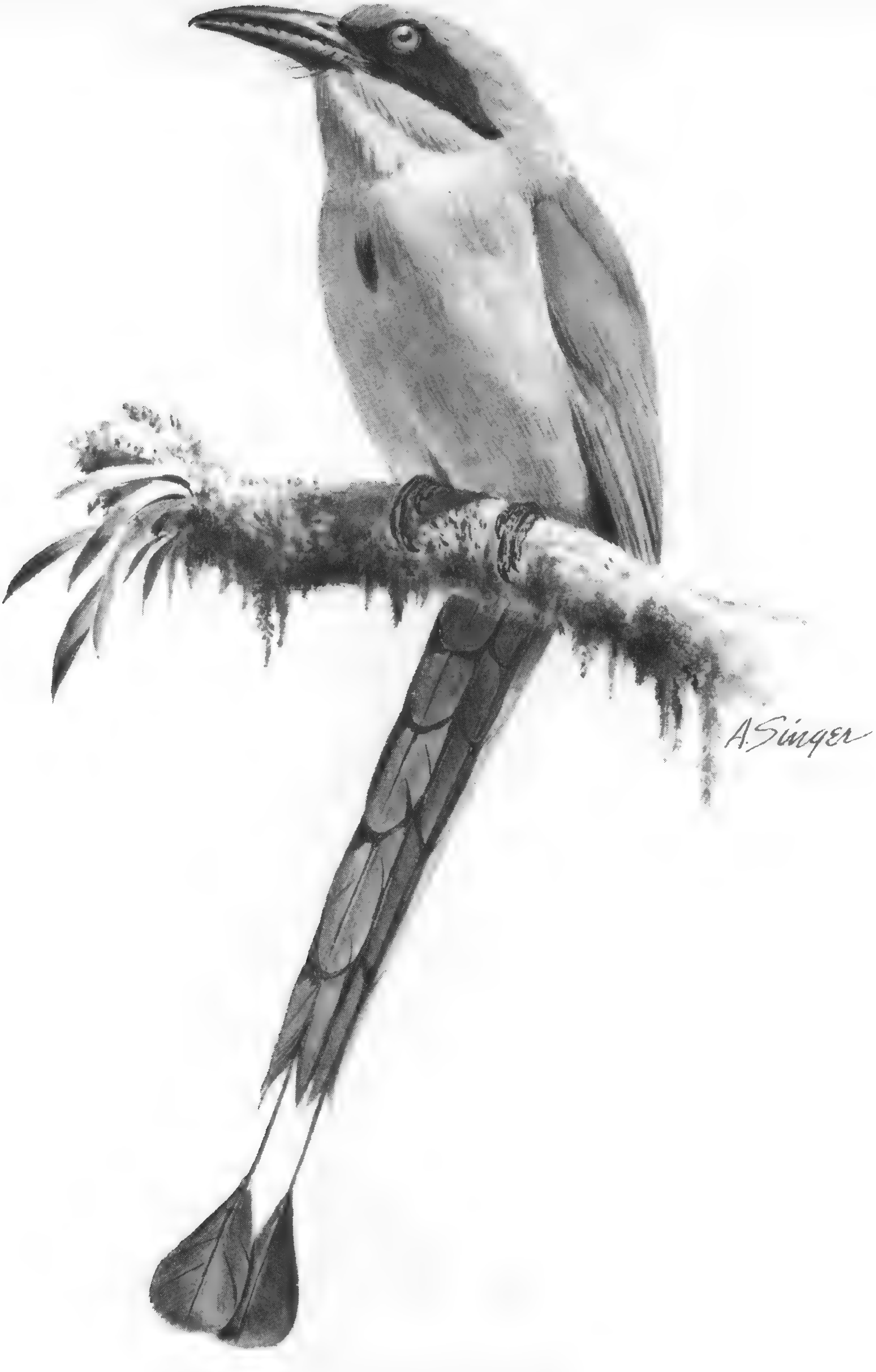
I saw no overt competition between the two species when both occurred at a swarm, even when several manakins were present, and I saw no supplantings or attempts for the same prey items when the two species foraged together away from swarms. Between February and September when neither species follows swarms very often, any foraging opportunities provided by swarms for these types of birds must be unused.

TABLE 5

Attempts at Prey Capture by Seven Migrant Bird Species

		Location of prey							
Bird species		*Air*	*Leaf, Twig*	*Stem, Liana limb*	*Trunk*	*Ground root*	*Log*	*Unspecified*	*Total attempts*
Acadian Flycatcher	S[1]	147	83	18	22			12	282
	L[2]			2	1				3
Wood Thrush	S							1	1
	L		4			41			45
	T[3]					9			9
Swainson's Thrush	S	6	26	15	11	55		2	115
	L	1	8	9	2	147	2		169
	T					20			20
	D[4]					2			2
Gray-cheeked Thrush	S	2	4	3	3	3		1	16
	L		2	11	2	80	7		102
	T					5			5
Veery	S		1	3	6	1			11
	L	1		3		25			29
Kentucky Warbler	S	1	15	2		1			19
	L		20	4		78			102
Canada Warbler	S	15	27	1		3		4	50
	L		10	4	5				19

[1] Sallying. [2] Lunging. [3] Leaf tossing. [4] Digging.



Great Rufous Motmot, *Baryphthengus ruficapillus*. Drawing by Arthur Singer.

Away from swarms the resident Golden-crowned Spadebill (*Platyrinchus coronatus*), Ochre-bellied Flycatcher (*Pipromorpha oleaginea*), Ruddy-tailed Flycatcher (*Terenotriccus erythrurus*), and Olivaceous Flatbill (*Rhynchocyclus brevirostris*) forage the most like the Acadian Flycatcher. I have never seen supplantings or fights over food between these species. The small Spadebill tends to stay in moist forest along ravines, while the large Flatbill usually occupies liana-crowded secondary woodland around treefalls; both are habitats the Acadian Flycatcher seldom uses. The Ochre-bellied Flycatcher is local on Barro Colorado and eats more fruit than do the other species. The common Ruddy-tailed Flycatcher is much smaller than the Acadian and tends to sally shorter distances in the terminal foliage.

In general, the Acadian Flycatcher seems to exploit a food supply which is never used by any resident species to any significant extent. It uses essentially the same foraging behavior as in the United States, except for rather frequent ant-following during fall migration.

Acadian Flycatchers definitely preferred swarms of *Labidus praedator* to those of *Eciton burchelli* (Table 3). Generally the flycatchers stayed above swarms of the former species for long periods and wandered widely around swarms of *burchelli,* staying for short periods. Although more resident birds follow *burchelli,* competition did not seem to be a factor in the low attendance by Acadian Flycatchers. Probably the tendencies of *praedator* to flush small insects, to flush prey in small bushes, and to stay in one area were more important in attracting this species.

Yellow-bellied Flycatcher (*Empidonax flaviventris*). — Both the Yellow-bellied Flycatcher, which winters in the undergrowth of forests from Mexico to Panama, and the Acadian Flycatcher, which winters from Costa Rica to northern Ecuador and Venezuela, forage in the same way. Since neither gives its distinctive song very often in winter, field identification of these two species is difficult in Panama. Fortunately the deep *wreep* call of the two species instantly distinguishes them from other flycatchers of the genus wintering in Panama; the Traill's, Willow (*Empidonax brewsteri*), and Least (*E. minimus*) Flycatchers belong to the division of the genus with light, high *wit* notes. Flycatchers of the "wit" group generally winter in second growth and bushy pastures, not in the forest. The Yellow-bellied Flycatcher is normally much more yellow on wing-bars, around the eye, on the throat, and on the center underparts than are the "wreep" flycatchers on Barro Colorado which nearly always have whitish throats, eye-rings, and wing-bars and show a yellowish tinge to the flanks. The five specimens that I collected over swarms are Acadian Flycatchers, according to Ned K. Johnson. Probably most or all of the "wreep" flycatchers listed in the preceding account were Acadian Flycatchers. Perhaps the Yellow-bellied Flycatcher tends to winter at higher elevations or in lighter forest in the countries where it is supposed to winter with the Acadian Flycatcher.

I did not find Yellow-bellied Flycatchers at swarms in British Honduras, where it winters commonly; but I was present only in the spring months. By analogy with the Acadian Flycatcher, it may follow swarms commonly in the fall. A flycatcher which followed a swarm of *Eciton burchelli* for 18 minutes on Barro Colorado on 2 October 1961 had very greenish-yellow underparts and was perhaps the Yellow-bellied Flycatcher.

Turdidae

Thrushes are the most important species which follow driver ants in Africa (Chapin, 1932), and many species resident in the neotropical region also follow ants. For the most part, neotropical forest-inhabiting thrushes live in the highlands where army ants are rare or absent. In some areas, as on Trinidad where ant-following antbirds are absent, thrushes follow the ants on the lower slopes of mountains. Four northern thrushes of the genus *Hylocichla* are among the most important migratory species at swarms.

TABLE 6

Swarm Attendance by Wood Thrushes on Barro Colorado

	Ant species			
	Eciton burchelli		*Labidus praedator*	
Month	*Number of swarms*	*Number of Thrushes*	*Number of swarms*	*Number of Thrushes*
1960				
October	1 (3%)[1]	1		
November	7 (29)	7	9 (24%)[1]	12
December	2 (6)	3	3 (12)	3
1961				
January	3 (8)	3	3 (25)	3
February	2 (5)	2	5 (36)	7
March	3 (7)	3	2 (29)	3
October	1 (1)	1	3 (17)	3
November	1 (2)	1	1 (14)	1
1962				
January	2 (7)	2	1 (7)	1
1965				
January	2 (8)	2		
February	4 (6)	4		
Totals	28	29	27	33

[1] See Table 3 for the column headed "Swarms" which gives the denominators for these percentages.

Wood Thrush (*Hylocichla mustelina*). — I observed 62 individuals at 55 swarms on Barro Colorado (Table 6). The species usually flees as soon as it sees the observer, so that it may be more common at swarms than these records indicate. It followed swarms mainly in the fall of 1960, an unusually wet year when there were many swarms of *Labidus praedator*. The species rather frequently followed the few swarms of *praedator* which appeared in the following dry season, perhaps as a holdover of the searching pattern developed the preceding fall. Table 2 indicates that the species was generally more common in the winter of 1960-1961.

On Barro Colorado, I recorded Wood Thrushes from 26 October 1960 to 20 April 1961, and from 12 October 1961 on. The maximum number in one day was seven on 4 February 1961. The species is seen on more days in November than it is earlier or later in the season; numbers decrease gradually to April.

At or away from swarms this species waits on sturdy horizontal perches or hops on the forest floor. More frequently than any other migrant thrush it tosses dead leaves by swiping or by grabbing them with the bill. It seems to take prey in much the same way on its breeding grounds (Dilger, 1956a). However, at swarms it pecks at prey in or on the leaf litter more frequently than it does anything else (Tables 5 and 7).

TABLE 7

Heights of Perches and Attempts at Prey for Wood Thrushes

	Height in meters													
	0.1	*0.2*	*0.3*	*0.4*	*0.5*	*0.6*	*0.7*	*0.8*	*0.9*	*1.0*	*2*	*3*	*4*	*5*
Number of perches	86	25	3	3	3	2	2	3	1	1	4	1	1	2
Number of attempts	50	3	1											

The Wood Thrush nearly always hops well ahead of or to one side of an advancing swarm, and thus seldom comes into close contact with the resident antbirds over the better foraging zones near the ants. On three occasions Ocellated Antthrushes supplanted Wood Thrushes which had hopped near a swarm before the antthrushes arrived. Twice an unknown bird supplanted a Wood Thrush. One Wood Thrush supplanted a Swainson's Thrush; another supplanted a Kentucky Warbler. The custom of hopping at the periphery of swarms may keep the Wood Thrush away from the bites and stings of ants, but the fact that it sometimes moves in over swarms when competing antbirds are absent suggests that interspecific competition is a factor in restricting the species to a peripheral niche.

Intraspecific supplantings were recorded 14 times, 13 of them between two thrushes at a raid of *Labidus praedator* on 4 February 1961. The aggressor at this raid snapped the bill during one chase. Once it raised its crest before it supplanted the high and sleeked subordinate bird, which flicked its wings. When both birds waited above the ground they ignored each other. One bird performed foot-quivering as it looked at the ants. Dilger (1956b) in his studies on the nesting grounds did not record foot-quivering nor a sleeked posture for subordinate birds, but the other movements I noted are typical of low-intensity agonistic interactions on the nesting grounds.

The supposed absence of foot-quivering in Wood Thrushes was a major point in Dilger's argument that the Wood Thrush should be left in *Hylocichla* while the supposedly congeneric species should be transferred to *Catharus*. Pending a more complete study of the tropical species of *Catharus* as well as the nearctic *Hylocichla,* I am here following traditional taxonomic practice in keeping all the nearctic species in *Hylocichla.*

Normally only one Wood Thrush stays at a given swarm of ants, although the widest swarms may have a thrush at each end. Away from swarms one seldom sees two together. Silent chases when two do come together and the even distribution of birds suggest that they hold winter territories. The grunting *bup bup bup* and loud *whit whit whit* calls are occasionally heard, but song is rare.

Away from swarms on Barro Colorado, the Wood Thrush occupies a niche rather different from that of any resident species. The Scaly-throated Leafscraper (*Sclerurus guatemalensis*), an uncommon furnariid which tosses leaves on the forest floor, may be a competitor. However, leafscrapers generally ignore swarms of ants. They also dig much more deeply and systematically in the leaf litter than do Wood Thrushes.

The Black-faced Antthrush (*Formicarius analis*) walks about swarms of ants and elsewhere to peck at the leaf litter or toss leaves in forests between Mexico and southern Brazil. In ease of walking and capturing prey it seems much better adapted to this kind of foraging than is the Wood Thrush. It weighs a third more than the Wood Thrush, and surely must supplant it in any competitive interaction. It is common in secondary woodland in the Forest Reserve of the Canal Zone, on Buenavista Point, and on Bohio Peninsula. Wood Thrushes are rare in these areas. Once this antthrush was common on Barro Colorado, but in the past few years as the forest has matured it has disappeared. By contrast, the Wood Thrush must now be much commoner than previously; Eisenmann (1952) lists only two records prior to 1951. I suspect that the Wood Thrush took the opportunity to move in when increasing height of the forest reduced the supply of food or nesting sites to such an extent that the antthrush population could not breed and persist in such a small area. The disappearance of antthrushes indicates that the niche occupied by wintering Wood Thrushes on Barro Colorado is not good enough to permit a resident species to persist. Whether or not Wood Thrushes contributed to the disappearance of antthrushes or help prevent their recolonization is uncertain. The local distribution and competitive interactions of Wood Thrushes and Black-faced Antthrushes are worth intensive study.

Swainson's Thrush (*Hylocichla ustulata*).—I observed 188 individuals at 95 swarms on Barro Colorado (Table 8). In addition, I observed six at four swarms of *Eciton burchelli* at Golfito in southern Costa Rica from 25 to 28

TABLE 8

Swarm Attendance by Swainson's Thrushes on Barro Colorado

	Ant species			
	Eciton burchelli		*Labidus praedator*	
Month	*Number of swarms*	*Number of Thrushes*	*Number of swarms*	*Number of Thrushes*
1960				
October	11 (37%)[1]	30	10 (23%)[1]	24
November	16 (67)	37	26 (70)	55
December	3 (9)	3	3 (12)	3
1961				
January	1 (2)	1		
March	2 (5)	2		
April	7 (12)	8	1 (17)	1
May	2	2		
October	12 (15)	16	4 (22)	4
November	1 (2)	1		
1965				
February	1 (1)	1		
Totals	56	101	39	87

[1] See Table 3 for the column headed "Swarms" which gives the denominators for these percentages.

March 1961 and two at a swarm of *Labidus praedator* in the Canal Zone Forest Reserve on 2 November 1961.

On Barro Colorado the species was a common migrant between 13 October and 21 December in 1960, with peaks of 35 recorded per day in late October. It was uncommon from 16 March to 15 May in 1961, with at most four per day the second week in April. It was also uncommon, after one straggler on 19 September, from 10 October to 18 November 1961; the maximum was eight on 18 October. The species is rare in winter, yet common in the Cordillera Occidental of Colombia (Miller, 1963; pers. observ.) where it may occasionally follow the few swarms of *praedator* occurring at high elevations. I did not find it in the constantly humid lowlands nearby, at El Tigre, where army ants are common but are well attended by resident ant-following birds.

Away from swarms this species is more arboreal than other species of the genus, although at times it does hop and pause like a typical thrush on the forest floor or logs. It frequently visits berry bushes or fruiting trees as well as capturing insects by sallying or pecking. Some birds visit fruiting trees near active raids and ignore the ants, especially if many resident antbirds are present. Rather similar foraging behavior is characteristic of the species in the United States (Dilger, 1956a; pers. observ.).

TABLE 9

Heights of Perches and Attempts at Prey for Swainson's Thrushes

	Height in meters																
	0.1	*0.2*	*0.3*	*0.4*	*0.5*	*0.6*	*0.7*	*0.8*	*0.9*	*1.0*	*2*	*3*	*4*	*5*	*6*	*7*	*8*
Number of perches	309	34	34	45	29	22	12	20	13	21	79	8	6	2	3		2
Number of attempts	226	7	3	3	5	3	2	3	2	2	23	3	4				

At swarms the Swainson's Thrush is less arboreal than usual. It tends to stay on the ground around the periphery of a swarm but in zones fairly near sites of active flushing (Table 9). Still, it sallies from perch to ground or vegetation more frequently than does any other member of its genus (Table 5). It is not limited to perches of small diameter, and it tends to take horizontal perches rather than use the vertical perches more common near the forest floor. When on vertical perches it often slides, flutters, or departs quickly. It leaves the low perches over the ants for the antbirds and other species better adapted for vertical perching.

One Swainson's Thrush, collected near a swarm of *praedator* in the Forest Reserve, 2 November 1961, had a roach and several unidentified concretions in its stomach.

Intraspecific supplantings and disputes are relatively infrequent among the migrant Swainson's Thrushes at swarms of army ants (Table 10). Where ants are flushing prey actively, the thrushes hop within a few centimeters of each other. On 12 November 1961, five of these thrushes hopped within a circle two meters in diameter at the edge of a swarm of *praedator*. On 17 November 1961, three Swainson's Thrushes at a raid of *burchelli* supplanted each other at times. One performed foot-quivering as it shivered its body, then tossed a leaf as if foraging. Possibly Swainson's Thrushes set up territories when on their wintering grounds (see Miller, 1963), but on migration

TABLE 10

Displacings and Supplantings of Swainson's and Gray-cheeked Thrushes

Supplanter	*Swainson's Thrush*		*Gray-cheeked Thrush*	
	Number of times	*Per cent*	*Number of times*	*Per cent*
Bicolored Antbird	70	49.6	14	43.7
Ocellated Antthrush	16	11.4	3	9.4
Gray-cheeked Thrush			6	18.8
Swainson's Thrush	16	11.4		
Squirrel Cuckoo	10	7.1	3	9.4
Spotted Antbird			2	6.2
Gray-headed Tanager	8	5.7	1	3.1
Plain-brown Woodcreeper	6	4.3		
Buff-throated Woodcreeper	4	2.8	1	3.1
Great Rufous Motmot	3	2.1	1	3.1
Bright-rumped Attila			1	3.1
White-throated Robin	2	1.4		
Coatimundi (*Nasua narica*)	2	1.4		
Slaty Antshrike	1	0.7		
Unknown	3	2.1		
Totals	141	100.0	32	100.0

they are dispersed or clumped so irregularly that they probably are not territorial.

Four Swainson's Thrushes, one Wood Thrush, three Gray-cheeked Thrushes, and two Veeries attended a swarm of *praedator* on 8 November 1961. These Swainson's Thrushes performed much single and double wing-flashing and foot-quivering. At this and other swarms with many thrushes they uttered growling *nyaa 'a 'ah* calls and fragments of song as well as the more usual *pirt* of alarm (with wing-flitting) or the buzzy *pernn* as in nocturnal migration. At this swarm one did a horizontal stretch with gaping at a Veery, which gaped from a withdrawn posture but did not flee (see Dilger, 1956b, bottom page 323, for a picture of a similar incident). In the relatively uncommon supplanting attacks between thrushes at swarms, Swainson's chased Gray-cheeked Thrushes five times out of six and displaced Veeries twice. Once a Wood Thrush supplanted a Swainson's Thrush. The Wood Thrush is much larger than the other species; but the Veery weighs slightly more than the Swainson's Thrush and the latter slightly more than the Gray-cheeked Thrush (Dilger, 1956a). Once a Swainson's Thrush supplanted a Kentucky Warbler.

Swainson's Thrushes supplanted Spotted Antbirds three times out of four, but the two species generally ignored each other. Spotted Antbirds, about half the weight of Swainson's Thrushes, would seem to be prime candidates for supplanting if the thrushes were to displace resident species at swarms. However, even when thrushes of several species crowded in at swarms in the fall or 1960, there were few which moved near antbirds. Bicolored Antbirds, which weigh slightly less than Swainson's Thrushes, supplanted them snappishly at such times. Instead of circling and returning, as another Bicolored Antbird would do if supplanted, the thrushes seemed completely cowed by the attacks. They moved peripherally or deserted the raids. At times of high numbers of thrushes, when the Swainson's Thrushes were numerous, they converged on swarms as soon as Bicolored Antbirds drifted off to loaf or preen; but thrushes were decidedly subordinate in encounters with other ant-following species as well (Table 10). Their foraging beat was restricted to whatever niches were not filled by resident birds, even during the period of greatest abundance and most persistent envelopment and intrusion on swarms in late October and early November, 1960.

Swainson's Thrushes attended swarms of *burchelli* much less frequently than swarms of *praedator*. Their rarity at swarms of *burchelli* was probably caused by high numbers and aggressive behavior of resident birds. Swarms of *burchelli* undoubtedly flush many insects of the large size suitable for a large bird like a thrush.

Gray-cheeked Thrush (*Hylocichla minima*). — I observed 85 individuals at 63 swarms on Barro Colorado (Table 11). In addition, one briefly visited a swarm of *Eciton burchelli* at Remedios, Colombia, on 6 May 1962. Attendance on Barro Colorado was primarily at swarms of *Labidus praedator,* where the thrush stayed and foraged persistently rather than hopping away after a few minutes as was commonly the case at swarms of *burchelli.*

Gray-cheeked Thrushes were fairly common on Barro Colorado between 5 October and 3 December 1960; I recorded a maximum of 15 on 1 November. In 1961, migrants were uncommon from 12 October to 24 November. I saw single birds on 25 January, 4 February, and 15 April 1961.

At or away from swarms this thrush usually hops over the forest floor, pausing now and then in an upright pose or hopping rapidly to peck some prey from the leaf litter. At times it visits fruiting bushes or pecks prey off

TABLE 11

Swarm Attendance by Gray-cheeked Thrushes on Barro Colorado

Month	*Ant species*			
	Eciton burchelli		*Labidus praedator*	
	Number of swarms	*Number of Thrushes*	*Number of swarms*	*Number of Thrushes*
1960				
October	9 (30%)[1]	14	8 (19%)[1]	12
November	3 (12)	3	20 (54)	30
December	2 (6)	2	2 (8)	2
1961				
February			1 (7)	1
October	6 (8)	6	6 (33)	9
November	5 (10)	5	1 (14)	1
Totals	25	30	38	55

[1] See Table 3 for the column headed "Swarms" which gives the denominators for these percentages.

vegetation above the ground. At swarms it perches on or near the ground much of the time (Table 12), pecking from low objects more often than it sallies to surfaces above the ground (Table 5). It is less variable and opportunistic in its foraging zones than is the Swainson's Thrush. Like thrushes in general, the Gray-cheeked Thrush stands mainly on horizontal perches when above the ground. Except for ant-following behavior, it forages in much the same way as it does in migration and on its breeding grounds.

One Gray-cheeked Thrush, collected near a raid of *praedator,* had seeds of two different kinds of fruit and the remains of a sowbug and a beetle in its stomach.

TABLE 12

Heights of Perches and Attempts at Prey for Gray-cheeked Thrushes

	Height in meters											
	0.1	*0.2*	*0.3*	*0.4*	*0.5*	*0.6*	*0.7*	*0.8*	*0.9*	*1.0*	*2*	*3*
Number of perches	192	25	15	19	7	5	3	7	–	2	12	–
Number of attempts	90	8	1	1	1	2	–	8	–	1	3	1

At ant swarms this species tolerates other individuals of its species during migration. Sometimes two or three hop within a meter of each other without conflict. On 10 November 1961, however, two exchanged rasping *peeyaa 'a 'ah* calls for a time before one supplanted the other. The descending *feeyou* and slight tail-raising as birds flit their wings at swarms seem to be reactions to the observer rather than hostile calls at other thrushes. I noted no song or other suggestion of territoriality.

In the flocks of thrushes, which crowded around swarms in the fall of 1960, the Gray-cheeked Thrush generally ignored other species. Once it supplanted a Veery. On five out of six occasions Swainson's Thrushes supplanted it. Once a Gray-cheeked Thrush supplanted the much smaller Spotted Antbird, a resident which also wanders on the periphery of swarms. Twice the Spotted Antbird supplanted the thrush. It was quite unsuccessful at forcing its way near swarms when the aggressive Bicolored Antbirds and Ocellated Antthrushes were present (Table 10). At such times the Gray-cheeked Thrush was even more retiring than are Swainson's Thrushes, which took the brunt of attacks by resident ant-following birds. Their foraging zones were thus restricted to areas unutilized by either resident birds or Swainson's Thrushes. In the fall of 1960, a wet year with many swarms of *praedator,* there were many such areas. In the normally rainy year of 1961 there were fewer openings because there were fewer swarms of *praedator.* The migration and use of swarms by Gray-cheeked Thrushes dropped off sharply by November in 1961.

Veery (*Hylocichla fuscescens*). — I recorded 23 individuals at 22 swarms on Barro Colorado (Table 13). At only two swarms of *Eciton burchelli,* both in 1960, did one stay more than five minutes; at nine swarms of *Labidus praedator* the individuals foraged near the raids for more than five minutes each.

The Veery was uncommon on Barro Colorado from 16 October to 13 November in 1960 and rare from 20 September to 11 October in 1961.

Away from swarms Veeries usually flushed from the ground or from low perches. At swarms they hopped on the ground with other thrushes or waited silently on low perches. Of 16 records of perch angle, 10 were below 20 degrees, 3 between 20 and 40 degrees, and 3 between 40 and 60 degrees. The Veery usually captured its prey by pecking at the leaf litter on the periphery of a swarm, but took a fair proportion of prey by sallying like a flycatcher, especially to the trunks of trees (Table 5). Veeries in the United States spend more time sallying to the ground (Dilger, 1956a) than did these birds at ant swarms. My observations of migrating Veeries in the United States indicate only that the species works near or on the ground more than it forages arboreally.

TABLE 13

Swarm Attendance by Veeries on Barro Colorado

Month	*Ant species* *Eciton burchelli* *Number of swarms*	 *Eciton burchelli* *Number of Veeries*	 *Labidus praedator* *Number of swarms*	 *Labidus praedator* *Number of Veeries*
1960				
October	2	2	5	5
November	3	3	7	8
1961				
September	2	2		
October	3	3		
Totals	10	10	12	13

I have never seen intraspecific hostility at or away from swarms for this unassuming species. Of all the thrushes which follow ants, it is the least aggressive. Swainson's Thrushes supplanted it twice, a Gray-cheeked Thrush once. A Bicolored Antbird and a Gray-headed Tanager supplanted it once each. Even the small Spotted Antbird, half the size of the Veery, supplanted it twice. The Veery hopped or waited well away from the main swarm most of the time, so that it rarely came in contact with native or migrant ant-followers. In the groups of several species of thrushes which followed ants in the fall of 1960, the Veery usually remained near the periphery with Gray-cheeked Thrushes rather than with Swainson's Thrushes.

In 1961, when the number of raids of *Labidus praedator* was low and numbers of resident ant-following birds generally high at swarms of *Eciton burchelli,* the Veery briefly attended a few swarms early in the period of migration and was not seen at swarms after October 11. In the wet fall of 1960, by contrast, I recorded Veeries at ant swarms only after October 16. The difference between the two periods suggests that Veeries move in to swarms and stay in an area like Barro Colorado only when unusually high numbers of swarms of *praedator* or other food sources reduce the competition from domineering resident birds.

Vireonidae

Normally migrant and resident vireos forage high in the trees, at edges of the forest, and in scrub rather than in places frequented by army ants. A Yellow-throated Vireo (*Vireo flavifrons*) foraging near the ground on Barro Colorado, 17 December 1960, ignored a nearby active swarm of *Eciton* *burchelli.* Yellow-throated Vireos are fairly common migrants and uncommon winter visitors in the treetops on Barro Colorado.

Parulidae

Most migratory wood warblers winter in the highlands, where resident wood warblers are common but army ants rare. A few species of warblers, which winter in the lowland forests in the middle levels and crowns of trees, visit swarms infrequently. Three other species, which frequent the lower levels, visit swarms regularly, while three others (the *Seiurus* species) usually ignore swarms.

Chestnut-sided Warbler (*Dendroica pensylvanica*). — This warbler, a regular but uncommon winter resident on Barro Colorado, I recorded from 8 October 1960 to 17 April 1961. On several occasions one foraging in the midlevels of the forest with a wandering interspecific flock ignored a nearby swarm of ants. The species flutters after tiny insects on leaves and twigs, which are generally absent near the ants because little light penetrates as far as the ground in tropical forests.

Bay-breasted Warbler (*Dendroica castanea*). — Six individuals visited four swarms of *Labidus praedator* on Barro Colorado, 24 to 31 October 1960 and on 25 October 1961, when the ants briefly swarmed up on low shrubs and treefalls. Normally this species forages with wandering interspecific flocks in the midlevels of the forest and ignores swarms of ants. The horizontal twigs along which it hops and pecks nearby leaves are usually almost absent in zones frequented by army ants. This warbler is a common fall migrant and uncommon winter visitor on Barro Colorado, recorded from 16 October 1960 to 21 April 1961; a maximum of 10 was recorded on 24 October 1960.

Ovenbird (*Seiurus aurocapillus*). — On Barro Colorado this species normally forages by walking along the ground and pecking here and there. One would expect it to follow ants, but it normally ignores them. On 17 November 1961, one stayed briefly at a swarm of *Eciton burchelli.* It is a rare migrant and winter visitor on Barro Colorado.

Northern Waterthrush (*Seiurus noveboracensis*).—I recorded this species at swarms of *Eciton burchelli,* once on Barro Colorado (29 November 1960) and once at Simla, Trinidad (1 December 1961). Once in the Canal Zone Forest Reserve (2 November 1961) and twice on Barro Colorado (4 February and 3 March 1961) it was at swarms of *Labidus praedator.* The latter two records probably were the same wintering bird, because both were at the same location in the dry woods near the summit of the island.

The Northern Waterthrush walks on the leaf litter, pecking here and there, in relatively dry areas as well as along streams. It is so shy that it may occur at swarms more frequently than I recorded. The birds I watched from concealment had the habit generally of picking up a few insects and then walking away from the swarms rather than following ants persistently. On Barro Colorado the Northern Waterthrush is an uncommon to rare migrant and winter visitor, recorded 5 October 1960 to 23 April 1961.

Louisiana Waterthrush (*Seiurus motacilla*). — Individuals of this species on Barro Colorado ignored the ants on three occasions when swarms passed by. There the species is an uncommon winter resident. One bird, watched closely near a swarm of ants, walked and tossed leaves here and there by grasping them in the tip of its bill. It also pushed strips of bark off a rotten log with its bill and pulled off a few fragments of rotten wood by grasping and twisting with the bill. The tendency of this species to stay beside rocky streams insures that it could not follow ants persistently, although it may do so casually when ants cross streams. Slud (1964) has found the Louisiana Waterthrush at swarms in Costa Rica.

Kentucky Warbler (*Oporornis formosus*).—I recorded 171 individuals at 159 swarms on Barro Colorado (Table 14). One visited a swarm of *Labidus praedator* on Buenavista Point, Canal Zone, on 23 October 1960. Two others visited a swarm of *praedator* in the Canal Zone Forest Reserve on 9 November 1961. Five visited three swarms of *Eciton burchelli* on the Bohio Peninsula, Canal Zone, in February of 1962. One visited a swarm of *burchelli* by the Rio Agua Salud, Canal Zone, on 10 February 1965. In the spring of 1957, I recorded several at swarms at Gallon Jug, British Honduras. Since these warblers are shy and wander widely around swarms, they may occur more frequently. However, the chipping note of alarm usually calls attention to this bird.

The species is a common fall migrant and fairly common winter visitor on Barro Colorado (Table 2). I recorded it from 4 September 1960 to 18 April 1961; the maximum was 10 on 24 October 1960.

TABLE 14

Swarm Attendance by Kentucky Warblers on Barro Colorado

	Ant species			
Month	*Eciton burchelli*		*Labidus praedator*	
	Number of swarms	*Number of Warblers*	*Number of swarms*	*Number of Warblers*
1960				
October	6 (20%)[1]	6	6 (14%)[1]	6
November	10 (42)	11	15 (41)	16
December	16 (50)	18	6 (24)	6
1961				
January	2 (5)	2	5 (24)	5
February	4 (9)	4	2 (14)	2
March	14 (31)	15	2 (28)	2
April	1	1		
September	3	3		
October	20 (26)	20	4 (22)	4
November	2 (4)	2		
1962				
January	5 (17)	6	4 (29)	5
February	3 (12)	3		
1965				
January	8 (31)	9	3 (33)	4
February	15 (22)	18	3 (33)	3
Totals	109	118	50	53

[1] See Table 3 for the column headed "Swarms" which gives the denominators for these percentages.

At or away from swarms, individuals hop along the ground or over low lianas and logs, pecking tiny insects from the top of the leaf litter or from low vegetation (Tables 5 and 15). When this warbler perches briefly above the ground, it prefers horizontal perches; of 38 records, 19 were at an angle under 20 degrees from the horizontal, 5 were from 20 to 40 degrees, 6 from 40 to 60 degrees, 4 from 60 to 80 degrees, and 4 from 80 to 100 degrees. In a very common foraging maneuver this species hops or hop-flutters vertically upward from the ground, snapping prey from the lower side of a leaf, then drops to the ground to continue hopping. When no swarms are available, the species commonly joins the wandering mixed flocks of forest birds. At swarms the warbler usually wanders ahead or to one side of the swarm rather than working over the ants, but it often stays near a swarm for long periods.

TABLE 15

Heights of Perches and Attempts at Prey for Kentucky Warblers

	Height in meters											
	0.1	*0.2*	*0.3*	*0.4*	*0.5*	*0.6*	*0.7*	*0.8*	*0.9*	*1.0*	*2*	*3*
Number of perches	305	28	9	15	4	4	1	3	1	–	2	1
Number of attemps	92	14	4	3	1	–	–	1	–	–	1	–

One Kentucky Warbler, collected in the Forest Reserve on 9 November 1961 at a swarm of *praedator,* had in its stomach a collembolan (Poduridae), a bug (Dipsocoridae), a thrip, four ants (not *L. praedator*), a beetle, and a sowbug. All the insects were tiny, 1 to 3 mm in length.

Praedator should flush more small prey of interest to this small species, but the bird seems to follow swarms of *burchelli* frequently and persistently. Of the 118 Kentucky Warblers, 89 per cent stayed more than five minutes each at raids of *burchelli;* of the 53 at swarms of *praedator,* 92 per cent stayed more than five minutes each.

Normally individuals scatter so evenly through the forest that they may be territorial. At times, especially when the warblers first arrive in the fall, two birds chip repeatedly back and forth as if using the calls as territorial warnings. When two warblers are at the same raid, they usually hop at separate forks or at separate ends of the raid. I saw two hop within one meter of each other at a raid of *praedator* on November 11, 1960. On two other occasions one chased another off with a series of chipping notes.

The Kentucky Warbler normally keeps well out of the way of competing resident and migrant species, usually staying even farther from raids than do the migrant thrushes. Once a Swainson's Thrush supplanted one. Three times an Ocellated Antthrush supplanted a Kentucky Warbler which happened to hop near a raid; twice a Bicolored Antbird supplanted one.

Once a White-bellied Antbird (*Myrmeciza longipes*), a hopping species that forages at swarms like a Kentucky Warbler, supplanted the species in the Forest Reserve. The two species ignored each other at the swarm on Buenavista Point, Canal Zone, where fewer resident ant-followers were present. The White-bellied Antbird is absent in the high forest on Barro Colorado, except in tangles along the lake shore. It is so restricted to low and dense second growth that it is unlikely to compete significantly with Kentucky Warblers, which rarely go far from woodland or forest into low second growth. Moreover, the Kentucky Warbler never tosses leaves persistently when away from ants as does the White-bellied Antbird.

Six times on Barro Colorado and once in the Forest Reserve Spotted Antbirds supplanted Kentucky Warblers. The Spotted Antbirds forage over the ants when few Bicolored Antbirds or Ocellated Antthrushes are present, but move peripherally when the two larger species move in. At such times the Spotted Antbirds come near the Kentucky Warblers. Normally the slightly larger Spotted Antbirds forage by sallying to the ground or to vegetation above the level of the Kentucky Warbler, but the differences in methods of foraging leave an overlap zone. At times the Kentucky Warbler deserts the raid when a Spotted Antbird moves in or supplants it, but normally it simply hops to another side of the raid. It is thus restricted to spaces unoccupied by resident species around the raid, even though its foraging behavior seems to be rather distinct from that of the resident ant-followers.

On Barro Colorado there is no other species which forages like a Kentucky Warbler away from swarms. The Spotted Antbird away from swarms commonly forages by sallying to the ground for small prey, and must take some prey items of interest to Kentucky Warblers. Kentucky Warblers often associate with or follow Spotted Antbirds for minutes at a time, whether or not the latter are associating with a wandering interspecific flock. The frequency of the association suggests that Kentucky Warblers associate the Spotted Antbirds with ant swarms. However, I have never seen supplantings between these two species away from swarms.

The Nightingale Wren (*Microcerculus philomela*), which once occurred on Barro Colorado (Eisenmann, 1952) but disappeared as the forest became more mature, forages much like a Kentucky Warbler. Nightingale Wrens occasionally follow ants, but not as persistently or frequently as do Kentucky Warblers. The interactions and comparative local distributions of these two species are worth intensive study, perhaps in the Canal Zone Forest Reserve where both species occur. As is the case for Wood Thrushes and Black-faced Antthrushes, the disappearance of the resident species on Barro Colorado suggests that the niche now taken by the migrant species will not support breeding by the resident species.

Hooded Warbler (*Wilsonia citrina*) — Seven individuals attended seven swarms at Gallon Jug, British Honduras, between 14 March and 9 April 1957. This warbler, common in spring, flutters from one perch to another near the ground and darts up or down periodically after tiny prey on the ground or on low vegetation. It follows ants for long periods. In its foraging behavior it is practically a counterpart of the Spotted Antbird, which extends north only to Honduras. However, Hooded Warblers usually take horizontal perches; Spotted Antbirds often cling to vertical perches. The Hooded Warbler seems to be rare or absent as a winter resident wherever the Spotted Antbird resides, so that competitive exclusion may occur in overlap zones between Panama and Honduras.

Canada Warblers (*Wilsonia canadensis*). — I recorded 48 individuals at 37 swarms on Barro Colorado (Table 16). In addition, I recorded one on 29 September 1961 at a swarm of *Labidus praedator* in the Forest Reserve.

On Barro Colorado this warbler was a common fall migrant from 29 September to 5 November 1960 and 8 September to 8 November 1961; maxima of 12 and nine were recorded on 3 October 1960 and 19 October 1961. It was a fairly common spring migrant, 9 April to 15 May 1961, with a maximum of six on April 19. I found it wintering commonly in the highlands of

TABLE 16

Swarm Attendance by Canada Warblers on Barro Colorado

Month	*Ant species*			
	Eciton burchelli		*Labidus praedator*	
	Number of swarms	*Number of Warblers*	*Number of swarms*	*Number of Warblers*
1960				
October	4 (13%)[1]	4	8 (19%)[1]	11
November			2	2
1961				
April	2	2		
May	1	1		
September	1	1		
October	15 (19)	20	2 (11)	5
November	1	1	1	1
Totals	24	29	13	19

[1] See Table 3 for the column headed "Swarms" which gives the denominators for these percentages.

Colombia (see also Miller, 1963), where army ants are rare, and rare in the nearby lowlands, where army ants and resident ant-following birds are common.

At or away from swarms, the Canada Warbler dances along slender twigs at various angles to the vertical, reversing frequently as it flits the wings and jerks the tail periodically from 10 to 30 degrees above the horizontal. Away from swarms it forages from 2 to 10 meters above the ground most of the time, often joining the interspecific mixed flocks of the forest interior. At swarms it tends to forage lower, nearer the concentration of prey flushed by the ants (Table 17). Like many arboreal foragers, it uses a variety of foraging techniques (Table 5), sallying short distances to leaves or the air more often than pecking directly from the vegetation. It contorts its body, as if a bird drawn by Audubon, so supplely that it can peck underneath leaves below its own level.

There was no evidence of aggression between Canada Warblers, even when two to five birds foraged near each other at one swarm.

There is no other bird regularly following ants which is nearly as agile as the Canada Warbler at capturing small prey in and above the sparse vegetation that hangs low over swarms of ants. The Spotted Antbird, a larger

TABLE 17

Heights of Perches and Attempts at Prey for Canada Warblers

	Height in meters																
	0.1	*0.2*	*0.3*	*0.4*	*0.5*	*0.6*	*0.7*	*0.8*	*0.9*	*1.0*	*2*	*3*	*4*	*5*	*6*	*7*	*8*
Number of perches	3	8	16	21	25	19	13	17	18	13	102	58	17	6	3	3	1
Number of attempts	2	2	2	2	6	3	12	6	2	–	20	5	2	–	2	–	–

and clumsier species, flutters to vegetation in similar fashion when the aggressive Bicolored Antbirds or Ocellated Antthrushes prevent it from foraging near the ground. I saw only a few supplantings of Canada Warblers by other species: four by Bicolored Antbirds, two by Ocellated Antthrushes, one by a Spotted Antbird, one by a Plain-brown Woodcreeper, and one by a Bright-rumped Attila. Normally it forages above or on the periphery of raids rather than in the low and central zones of intense competition.

Away from swarms, Canada Warblers overlap in foraging behavior with the somewhat less agile White-flanked Antwrens (*Myrmotherula axillaris*), an abundant resident which seldom follows ants. Antwrens do not capture as many aerial prey as do Canada Warblers, and I never saw supplantings or competitive food chases involving the two species. However, competition from antwrens away from swarms may explain why Canada Warblers do not winter on Barro Colorado even though they differ rather strongly in their foraging from the resident birds that follow army ants.

Thraupidae

Although most tanagers are highland or treetop birds, a few forage low in tropical forests and encounter army ants. Resident ant-following species in Panama include the Red-throated Ant-Tanager (*Habia fuscicauda*) and the Gray-headed Tanager. Migratory species which usually stay in the treetops or at the edge of the forest seldom encounter ants.

Summer Tanager (*Piranga rubra*). — A male briefly came to 0.5 meter above the ground at an active swarm of *Eciton burchelli* on Barro Colorado, 27 October 1961. On the island the species was a fairly common migrant and uncommon winter visitor from 21 September 1960 to 20 April 1961; six birds were recorded 20 October 1960 and four on 5 April 1961, the maxima for the two periods of migration. The Summer Tanager favors the edges of the forest, where it flutters out on flycatching sallies or pecks at the foliage for large insects or fruit. The Plain-brown Woodcreeper occupies the niche that the Summer Tanager might take if it moved low enough within the forest to forage with ants.

Scarlet Tanager (*Piranga olivacea*). — A tailless and molting male visited two swarms of *Eciton burchelli* on Barro Colorado, 14 and 15 November 1961. The first day it sallied to a trunk at 6 meters above the ground and snapped off prey before leaving. The next day it came to limbs 0.4 to 2 meters above the swarm, then flew down and pecked in the leaves on the ground. It stayed with the swarm about 50 minutes but found little food. The few Bicolored Antbirds nearby were quarreling with each other and ignored the tanager.

I recorded one or two Scarlet Tanagers on a few dates from 16 October to 16 November 1960, on 13 April 1961, and 9 October to 15 November 1961. The species may be commoner, but I rarely looked in the treetops where it usually forages.

Seasonal and Yearly Changes on Barro Colorado

The percentages of migrant individuals at raids of the two army ants on Barro Colorado are given in Figure 1. Migrants were uncommon to rare except during fall migration. Generally migrants formed a greater percentage of the birds at swarms of *Labidus praedator* than they did at swarms of *Eciton burchelli*. Resident birds, which were most numerous at swarms in the same months as migrant birds, favor the raids of *burchelli*.

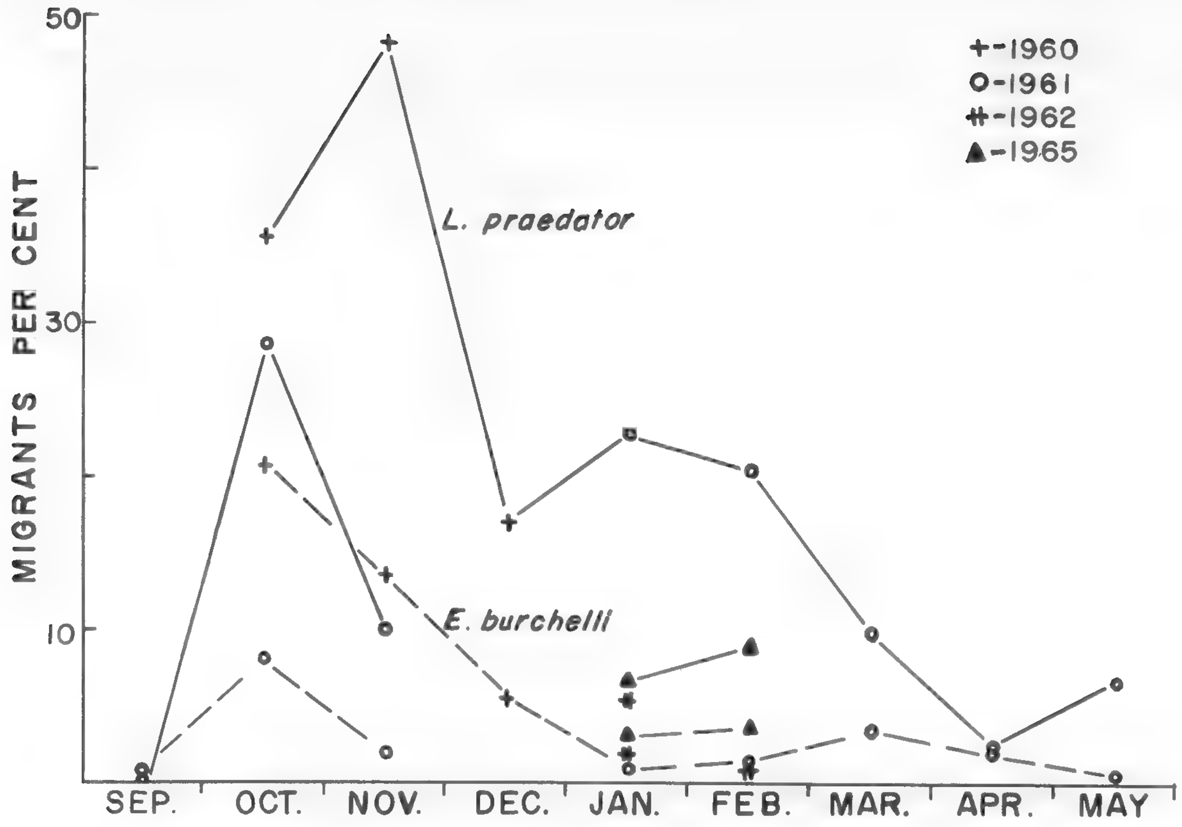


Figure 1. Percentages of migrant birds (individuals of all species) at swarms of two army ants, *Labidus praedator* and *Eciton burchelli,* on Barro Colorado Island, Canal Zone.

To compare the fall peaks of attendance in detail, I divided October and November of 1960 into four periods (1 to 15 and 16 to 31 October; 1 to 15 and 16 to 30 November) and added the period 1 to 31 December. I divided October of 1961 into two periods (1 to 15 and 16 to 31) and added the period 1 to 25 November. In the five periods in the fall of 1960, the percentages of birds which were migratory individuals at swarms of *praedator* were 7.6, 60.0, 51.5, 31.7, and 17.0. Percentages of migrants at swarms of *burchelli* during these periods were 1.7, 31.6, 22.2, 11.9, and 5.8. In 1961 the period 1 to 15 October was better than it had been in 1960, for 9.8 per cent of the individual birds at swarms of *praedator* and 8.5 per cent of those at swarms of *burchelli* were migrants. However, only 9.2 per cent of the individuals at swarms of *burchelli* and 36.9 per cent at the few raids of *praedator* were migrants between 16 and 31 October. The per cent of migrants then dropped to 2.0 at swarms of *burchelli* and 10.0 at raids of *praedator* for the period 1 to 25 November.

The average numbers of migrant birds per swarm of *burchelli* for the five periods in the fall of 1960 were 0.1, 4.1, 2.6, 3.1, and 1.3. In 1961, the averages were 0.9, 1.5, and 0.4 migrant per swarm. The average numbers of migrants at swarms of *praedator* were 0.2, 4.8, 5.1, 2.5, and 0.8 in the fall of 1960 and 1.0, 2.5, and 0.7 in the fall of 1961.

During these eight periods the density of the swarms of *burchelli* was about 2.5 per square kilometer, so that in the fall of 1960 there were 0.2, 10.0, 6.5, 7.8, and 3.2 migrants per square kilometer and in the fall of 1961 there were 2.2, 3.8, and 1.0 migrants per square kilometer at swarms of *burchelli.* Using estimates derived from strip censuses for densities of swarms of *praedator,* migrants at these swarms in the five periods in 1960 averaged 2.8, 67.2, 81.7, 40.0, and 7.2 per square kilometer while in the three periods in 1961 there were 11.0, 27.5, and 4.2 migrants per square kilometer.

Migrants thus followed swarms strongly well into November and even into January in 1960, but in 1961 an early movement to the swarms dwindled into relative insignificance in November. Could the contrast between these years be due to a general drop in numbers of migrants? Records from the "Operation Recovery" Program of the United States Fish and Wildlife Service, courtesy of Chandler S. Robbins, suggest the reverse for Gray-cheeked and Swainson's Thrushes, the two species mainly responsible for the change between 1960 and 1961 on Barro Colorado. At the three stations (Ocean City, Maryland; Cape May, New Jersey; Nantucket, Massachusetts) for which comparable data are available, less than half as many individuals of these two species were captured per net per hour in the fall of 1960 as in the fall of 1961. The efficiency of netting, as measured by numbers of birds of all species caught per net-hour, increased slightly at Ocean City and Cape May and decreased slightly at Nantucket between 1960 and 1961. Could thrushes have shifted from an interior route to a coastal one, causing the difference between 1960 and 1961 on Barro Colorado? The data from *Audubon Field Notes,* the only available source, do not indicate such a general and unlikely shift in the pattern of migration. George A. Hall, writing of the Central Appalachian Region in 1961 (*Audubon Field Notes,* 15:41) says that "the spotted thrushes, particularly the Swainson's, had a very good fall flight throughout the region." Since there is no evidence of a general drop in numbers or of a shift in migration patterns, another possibility is discussed below: that migrants used superabundant swarms of *praedator* in 1960 but had to go elsewhere in 1961.

Minor peaks in swarm-following, one migrant per 30 individuals at swarms, were recorded in March of 1961 and January and February of 1965. The latter high was associated with an unusually high number of swarms of *burchelli* (between 3 and 3.5 per square kilometer) and low attendance at each swarm by resident ant-following birds (Figure 2). The average numbers of migratory individuals per swarm of *burchelli* were 0.42 in January and 0.39 in February. Kentucky Warblers, unusually abundant in the winter of 1965 (Table 2), accounted for 71 per cent of the records in these two months.

The minor peak of March 1961 occurred in the face of a fairly high number of resident individuals at swarms, some 16.8 resident individuals per swarm of *burchelli* compared with 0.6 migrants per swarm. This high resulted from attendance by the three wintering ant-followers, the Acadian Flycatcher, Wood Thrush, and Kentucky Warbler. Only two of the 26 migrant birds recorded at swarms of *burchelli* in March were Swainson's Thrushes. Total numbers of the wintering species did not increase between February and March 1961 (Table 2). Spring migration, if it brought in new birds, must have been accompanied by departure or death of wintering birds.

Wood Thrushes and Acadian Flycatchers were more common in the winter of 1960 than in the winters of 1961 and 1965 (Table 2). However, Kentucky Warblers, which account for 15 of the 26 migrants in March of 1961, were about equally common in 1961 and 1962 and were even more common in 1965. Of course, data are lacking for March in 1962 and 1965; it is possible that Kentucky Warblers always move to the swarms in March, even in years of low density of warblers and despite high attendance by resident ant-following birds. Samples of insects from the leaf litter, taken semimonthly at five sites on Barro Colorado from late February to November in 1961, show lowest numbers of arthropods in March. Leaf litter samples on 14 February

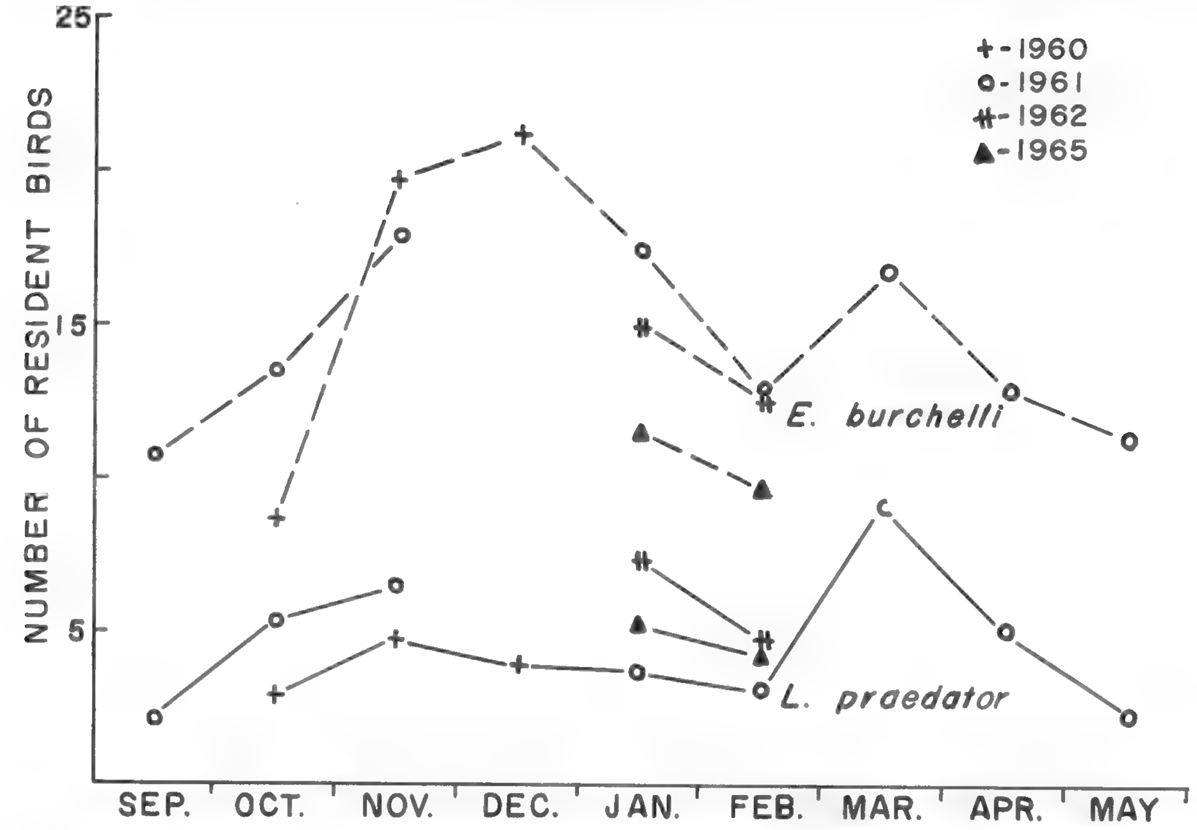


Figure 2. Number of resident ant-following birds (individuals per ant swarm) at swarms of two army ants, *Labidus praedator* and *Eciton burchelli,* on Barro Colorado Island, Canal Zone.

1962 produced more insects than samples taken on 28 February 1961, suggesting that the middle of the dry season of 1961 was a time of scarcity of arthropods. The rather high numbers of resident and migrant birds at swarms of army ants in March 1961 may reflect an unusually high survival of birds the preceding wet fall and an unusually low number of insects away from swarms by March.

Except for this slight peak in March there was little use of swarms by migrants in spring. Total numbers of migrants are, of course, lower during spring migration than in the fall (Table 2); but proportionately fewer migrants followed ants in spring than in the fall. Adding numbers for the seven species in Table 2, the per cent of migrant individuals which were at swarms was 14.6, 30.0, and 22.7 in October, November, and December 1960, respectively; the per cent at swarms was 17.2 and 14.2 for March and April 1961. There is variation from year to year; in October and November of 1960 the per cent of these migrants which were attending swarms was 24.0 and 10.0, respectively. We need more spring records to see if it is always true that proportionately fewer migrants follow swarms in spring.

Other Observations in Central America

From 23 to 25 September 1964, I observed birds near Chichén Itzá, Uxmal, and Progreso in Yucatán, Mexico. In the dry thorn scrub and low and bushy second growth of these areas, migrants were numerous and conspicuous by their fearlessness. None were at swarms of ants.

In 1957, I visited Gallon Jug, British Honduras, for a study of two species of ant-tanagers (Willis, 1960). Migrants common in the low and varied forests of this area include Yellow-bellied Flycatchers, Blue-gray Gnatcatchers

(*Polioptila caerulea*), Worm-eating Warblers (*Helmitheros vermivorus*), Kentucky Warblers, and Hooded Warblers. The latter two species followed swarms on several occasions. Migrants were similarly numerous at the edges of the forest, in scattered trees, and in second growth.

From 8 to 21 September 1964, I visited several areas in the central highlands of Costa Rica. I encountered no ant swarms in the only area low enough for them, at Cariblanco on the Rio Sarapiquí (10° 14′ N Lat.; 84° 10′ W Long.; 700 meters elevation). During my visit I encountered few migrants in forests but many at the edges of forests, in scattered trees, and in second growth throughout the highlands. Migrants were especially numerous in coffee groves in the central valley around San José, where native birds have practically disappeared.

In late March 1961, I visited Golfito, Costa Rica, in the tall rain forests fronting the Golfo Dulce. Migrants were not common either in the forest or at the edges of the forest, but a few Swainson's Thrushes visited the large colony of *Eciton burchelli* which I watched for four days. Slud (1964) records Swainson's Thrush, Bay-breasted Warbler, Northern Waterthrush, Louisiana Waterthrush, Canada Warbler, and Summer Tanager following swarms in Costa Rica.

In late February 1961, a visit to the highlands of Panama near Cerro Punta, Chiriquí, produced rather large numbers of migrants, especially Wilson's Warblers (*Wilsonia pusilla*). Migrants were generally restricted to coffee groves, second growth, and edges of the forest. None were in the tall, epiphyte-laden cloud forests, even in the large mixed flocks of furnariids, woodcreepers, bush-tanagers, and resident warblers. I located no swarms of ants at these elevations, 1,500 to 3,000 meters; the swarming ants are rare above 1,000 meters.

I occasionally visited several forested areas away from Barro Colorado in the Canal Zone during 1960, 1961, 1962, and 1965. Migrants were most common at the edges of forests and in second growth or semi-open areas. The relatively dry second growth of the Forest Reserve was especially good for migrants at swarms of ants.

In summary, the brief observations in Central America suggest that most of the migrant birds avoid the forests, where army ants are common, and instead occur in disturbed, patchy, or low to open habitat, especially in the highlands. At Gallon Jug, migrants were more numerous in fairly tall forest than they were in similar forests in Costa Rica and Panama. There may be more migrants within the forests to the north and hence more migrants at swarms of ants to the north.

Observations in South America

During 1961, 1962, 1965, and 1966 I studied ant-following and other birds in Colombia, Ecuador, Peru, Brazil, Trinidad, and British Guiana during months when migrants should be present. My chief finding was the remarkable absence of migrants from swarms of ants.

Records from western Colombia are especially noteworthy since several species of ant-followers winter in this region (de Schauensee, 1964): Acadian Flycatcher, Swainson's Thrush, Gray-cheeked Thrush, Kentucky Warbler, and Canada Warbler among others. I saw not one migrant at swarms or in the forest at El Tigre, at the western base of the Andes in the perpetually wet Chocó of Colombia, on my visit in late February and early March 1962. A few migrants, such as Summer Tanagers and Mourning Warblers, were seen at the edges of clearings or banana plantations; but, in general, migrants were much less common than they are on Barro Colorado at the same time of year.

From 9 to 28 March 1965, I visited several localities from Chigorodó (7° 41′ N Lat., 76° 41′ W Long.) to Tucurá (7° 56′ N Lat., 76° 16′ W Long.) across the northern end of the Cordillera Occidental of Colombia in a search for Sooty Ant-Tanagers (*Habia gutturalis*). Acadian Flycatchers, Great Crested Flycatchers, and Bay-breasted Warblers were fairly numerous in forests strongly affected by the dry season, as at San Pedro. Otherwise migrants were almost restricted to second growth and to the edges of forests, plantations, and watercourses in areas disturbed by man. Migrants seemed slightly less common than in similar areas in the nearby Panama Canal Zone. The only migrants at swarms were two Great Crested Flycatchers at San Pedro. Wood Thrushes and Kentucky Warblers, two species which regularly follow ants in March in the Canal Zone, were nowhere to be seen in northern Colombia.

From 12 to 31 March 1962, I visited Queremal and several other localities on the western slopes of the Cordillera Occidental in Colombia in an extended search for the elusive Crested Ant-Tanager (*Habia cristata*). At each location I watched for migratory species and recorded approximate numbers of these and resident species seen each day. There were no birds at the two swarms of *Labidus praedator* that I encountered. Although the highland forests in this area have been cut extensively, forests remain distant from the roads. I was able to visit many types of habitats between 600 and 2,200 meters elevation. At all elevations I found migrants numerous only in patches of second growth and at the edges of the forests. There were practically no migrants in areas of extensive forest, where native furnariids and other species are still common. I saw some Acadian Flycatchers and Swainson's Thrushes in disturbed forests, but they were not following ants.

The other areas that I visited in Colombia produced few migrants. I visited Remedios, at the northern end of the Cordillera Central, which has a rainfall similar to that at Tucurá and Barro Colorado, too late in the spring to expect many migrants; the few I did see were at the edges of forests and in second growth, except for one Gray-cheeked Thrush at a swarm of army ants. Tres Esquinas, east of the Andes in Amazonian Colombia, was extremely poor for migrants in the forests in April of 1962. Migrant swallows and sandpipers were common at the airport, while Blackpoll Warblers (*Dendroica striata*) were fairly numerous on burned tree trunks in forest clearings. Two Traill's Flycatchers were at a swarm in the bushy pasture near the airport.

At Simla and other localities in Trinidad, migrants were most common in second growth or at the edges of forest, by streams, or roads. A single Northern Waterthrush followed ants.

At Nappi Creek and other localities in British Guiana, migrants were almost absent even in normally favored localities, such as patches of second growth and scattered trees in man-disturbed areas. None followed ants.

From 12 October to 12 May 1966 I studied birds in the Amazonian lowlands of Ecuador, Peru, Brazil, and Colombia. There were practically no migrants in forests, except along the Andes in eastern Ecuador. Even there most migrants were in scattered bushes and trees in areas disturbed by man. Irregular patches of trees and bushes along rivers attracted such species as Sulphur-bellied Flycatchers (*Myiodynastes luteiventris*).

In Brazil, from 15 January to 18 April, I found migrants only along the rivers or in clearings. As one striking example, migrant swallows and flycatchers outnumbered resident birds over the beautiful blue Tapajoz River, a biological "desert," on my one trip up it (17 February). Migrants were common in clearings along the river, but I saw not one migrant among hundreds of species of resident birds in nearby forests from 15 January to 4 March.

The only migrants I recorded at ant swarms were 11 Swainson's Thrushes at 10 swarms of *Eciton burchelli,* a Canada Warbler at the first swarm, and a Gray-cheeked Thrush at an eleventh swarm, all between 20 October and 22 November in the Andean foothills of eastern Ecuador. All migrants were in second growth or at the edge of the forest except a Swainson's Thrush at three successive swarms, 21 to 23 October.

In summary, my observations in northern South America indicate that migrants stay out of the forest for the most part and that they seldom visit swarms of ants, especially in Amazonian and Pacific forests. They are numerous only in the highlands, in recently disturbed areas, or in open to semi-open habitats. These tendencies are even more striking in South America than to the north, perhaps because the general decline in numbers of migrants away from the source of migration in North America seems more marked for forest-inhabiting birds than it is for migrants inhabiting more open areas. The constantly wet lowland forests of the Pacific slope and the upper Amazon scarcely attract wintering birds. One might think this vast sea of green the perfect goal for forest-inhabiting migrants, but nearly all these species crowd into the narrow strips of forest in Central America and the West Indies. Even the edges of forest and second growth in many parts of the Amazonian lowlands are little used by migrants.

Discussion

On the infrequent occasions when migrant birds compete directly with resident birds at swarms of army ants, the resident birds nearly always win. The migrant birds are readily supplanted by the domineering and aggressive resident birds. Even the small Spotted Antbird supplants some thrushes twice its size. A few supplantings of Spotted Antbirds by migrant thrushes were the only exceptions to the rule that migrant species are subordinate at swarms. Even the larger thrushes forage peripherally and take little or no advantage of their ability to supplant Spotted Antbirds.

Migrant Birds Unassertive at Swarms

Migrants are unasserting at the swarms. They forage peripherally or above the zones occupied by the resident species when the latter are present. Migrants are supplanted vigorously when they move near the antbirds and woodcreepers at the best areas for food. Often the migrant deserts the swarm rather than circling and returning the way a subordinate antbird would do.

Because migrants are so unasserting, resident birds expend very little time or energy chasing them. Bicolored Antbirds and Ocellated Antthrushes kept Swainson's Thrushes, the only migrant species which crowded near resident birds, away from their foraging areas with a few supplantings and with grunting warnings which never interfered with foraging. Supplantings and displays among the resident antbirds take far more time and energy, particularly during intraspecific interactions, than do the relatively rare supplantings of the timorous migrants. There is no reason to think that resident birds neglect their own nests and eggs to any extent because they spend time excluding migrant birds; the theory of "aggressive neglect" (Hutchinson and MacArthur, 1959; Ripley, 1959) does not apply here.

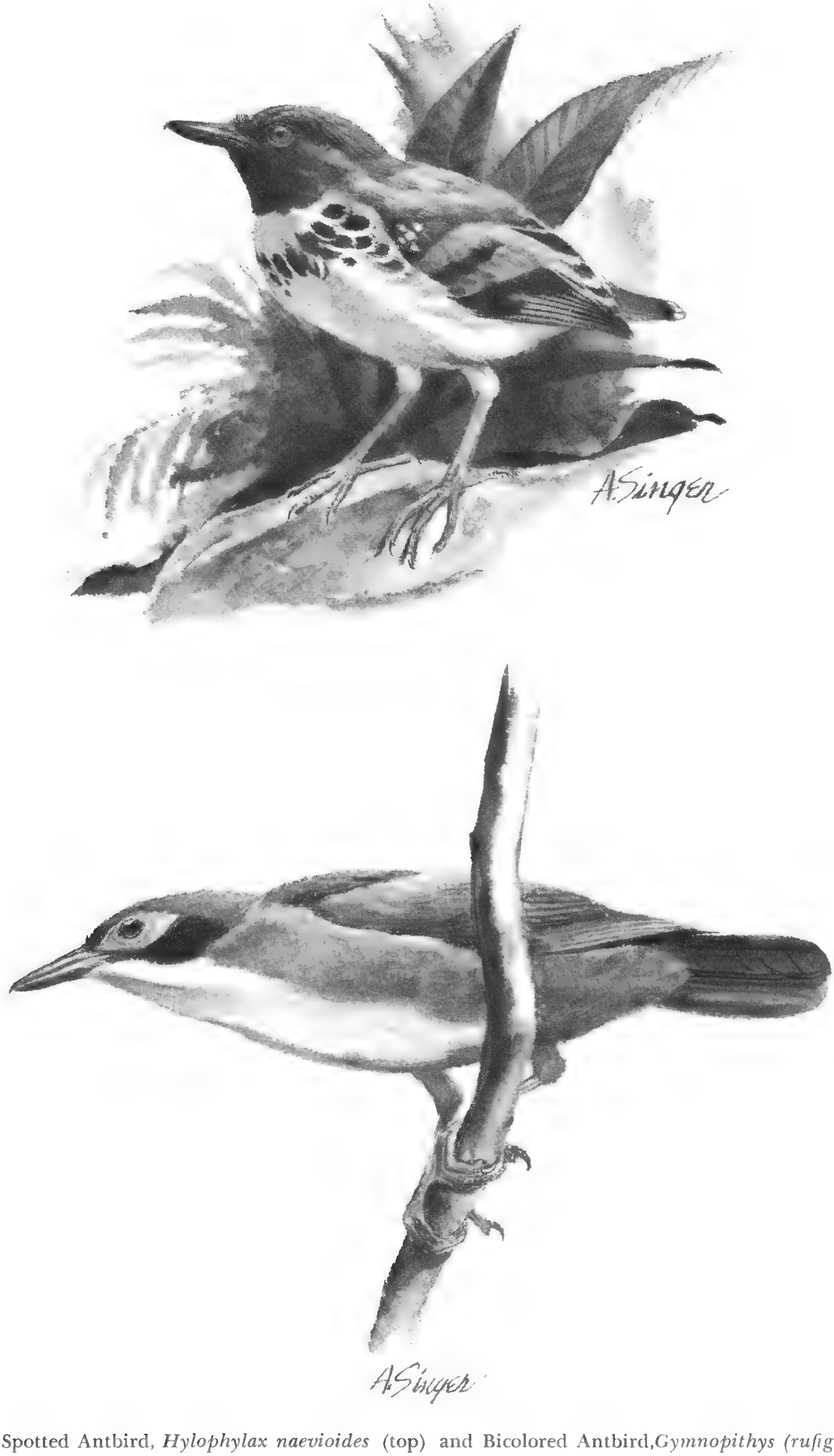
If migrants influence resident birds strongly, the resident species should stop nesting when migrants are most abundant, as Miller (1963) suggested for birds in a montane forest in Colombia. Instead, the antbirds which follow ants on Barro Colorado nest throughout the fall peak of migration. Individual Spotted Antbirds, Ocellated Antthrushes, and Bicolored Antbirds nest more or less continuously during the rainy season from April to December. The Plain-brown Woodcreeper probably nests during the same months, although perhaps less frequently after September.

The Gray-headed Tanager is the one regular ant-follower which definitely nests early in the year, from February to September. It, like the migrants, is a peripheral species at the swarms. It moves to the center when the domineering Ocellated Antthrushes are absent; when they are present, it forages at the occasional probes of ants up in the trees. However, Gray-headed Tanagers generally dominate Bicolored Antbirds, which dominate all migrant species. Any effect of the presence of migrants on nesting season should be on the Bicolored Antbird, not on Gray-headed Tanagers. The Gray-headed Tanager must stop nesting in September for some other reason than the fall influx of migrants. Since most other species of tanagers in the Central American lowlands also nest early in the year rather than during the peak of the rainy season, I suspect that tanagers find nesting during the rains difficult. Perhaps the fruits that resident tanagers eat more or less frequently are difficult to find after September; possibly the eggs or young of tanagers cannot stand exposure to rains; more probably the female, which in this family incubates and broods alone, cannot get enough food when rains interrupt foraging. There is no reason to assume that the hypothesis of competition with migrants is any better than any of the latter hypotheses at this time.

Do migrants restrict residents in some way which does not involve dominance? To win in a competitive situation, a subordinate bird must be more efficient; it must take food before its dominant competitor can do so. In this case there is practically no chance that migrants are capturing food that could later be taken by residents. The ants wander steadily, and swarms revisit a given location very infrequently. An insect which escapes birds is very likely to be eaten by ants or parasitized by flies which follow the ants. By the time some other swarm passes, the high rate of insect reproduction is almost certain to have replaced the few insects, which would have escaped the ants and flies, had they not been taken by a migrant. Of course, the depression of numbers of insects by migrants may not be completely rectified in all cases by the time swarms repeat in a given spot; and perhaps migrants away from swarms may reduce populations of arthropods throughout the forest so generally that resident antbirds at swarms do not capture as many insects. If either occurs, the populations of insects are being limited by predators rather than by the available food. However, swarms are ordinarily such cornucopias for the relatively small numbers of antbirds present that they spend much of their time loafing and preening. To offset any losses due to prior captures by migrants, they should only need to spend a little less time preening and a little more time foraging.

Migrant Birds at Swarms Forage Differently

In general, migrants at swarms on Barro Colorado forage differently than do resident species. Species which are winter visitors on Barro Colorado


A.Singer
A.Singer

Spotted Antbird, *Hylophylax naevioides* (top) and Bicolored Antbird, *Gymnopithys (rufigula) bicolor* (bottom) . Drawings by Arthur Singer.

rather than passage migrants are especially likely to differ in foraging from resident birds. Some winter residents, such as Acadian Flycatchers, Wood Thrushes, and Kentucky Warblers, attend swarms rather frequently and are rarely supplanted by resident species. Considering the overt competition for space within the narrow confines of swarms, this is a fair indication that the wintering birds are not competing with residents. Some passage migrants, especially Swainson's Thrushes, crowd in near the resident birds and capture prey near them to a greater extent than do the wintering birds; but, whenever the passage migrants do so for extended periods, the resident birds supplant and force them to peripheral foraging positions again. Other passage migrants, such as the Canada Warbler, differ from ant-following birds in foraging but are rather similar to resident species which do not follow ants. Possibly they would compete with these resident species away from swarms if they stayed all winter.

Migrant Birds Favor Swarms of *Labidus praedator*

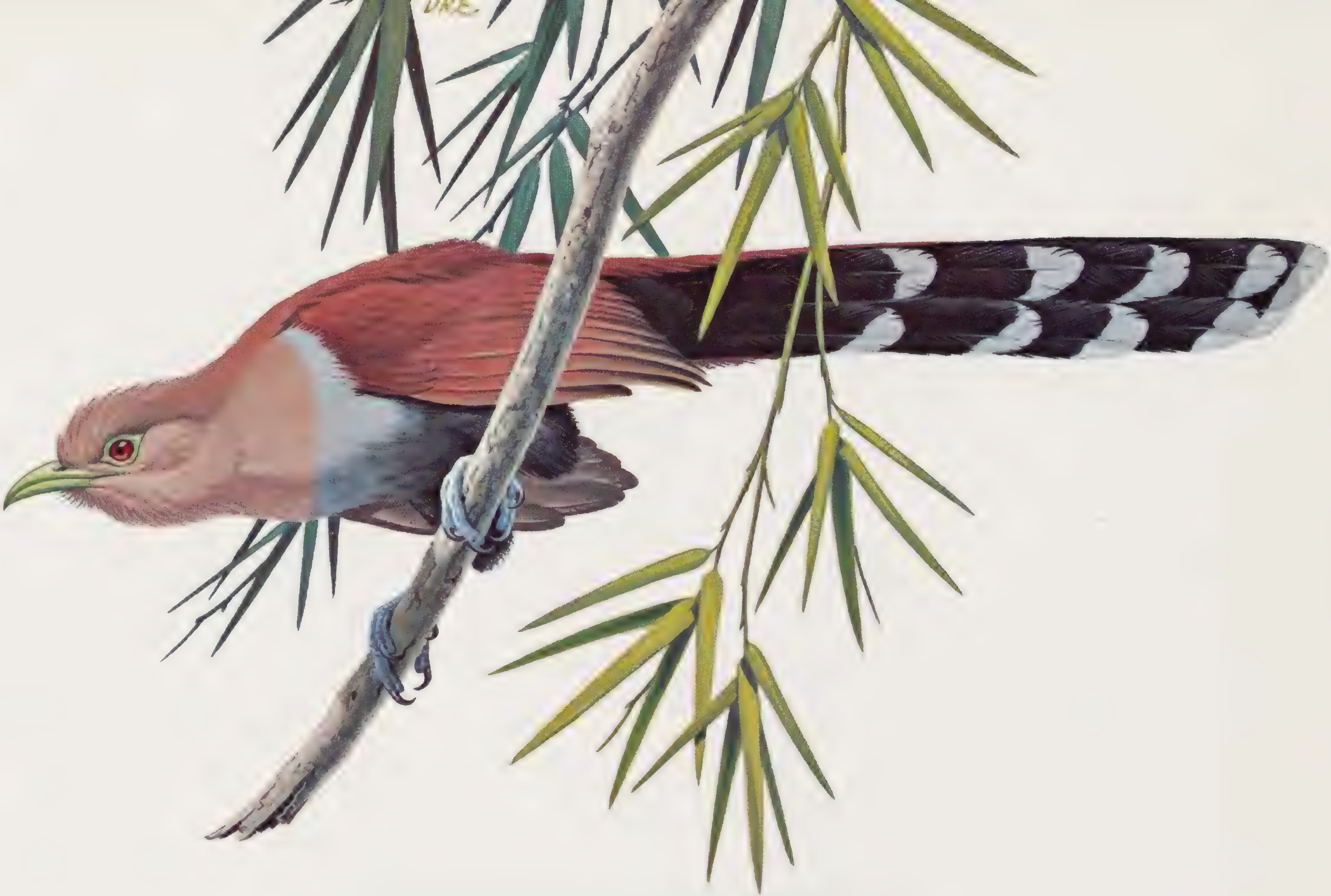
Migrant birds tend to follow swarms of *L. praedator* rather than the swarms of *Eciton burchelli,* which residents favor (Figures 1 and 2). Migrants favor *praedator* even though the average size of a raid of this species is about one third that of a raid of *burchelli.* Some species of migrants, notably the Acadian Flycatcher, may favor *praedator* because it flushes smaller prey and swarms at times over the leaves of low bushes. However, the large thrushes certainly should favor the large arthropods which *burchelli* flushes. It is unlikely that the larger size of ants of the latter species frighten the migrants, which always keep out of the way of the biting and stinging ants quite easily.

More probably there is such a striking contrast between resident and migrant birds because the domineering resident birds exclude migrants from swarms of *burchelli.* Two to ten times as many resident birds are at each swarm of the latter as at each swarm of *praedator.* Feuding and supplanting is much more frequent at most raids of *burchelli,* especially among the "professional" or consistent ant-followers. Migrants are supplanted more frequently at raids of *burchelli.* Kentucky and Canada Warblers and Wood Thrushes still find food on the periphery of raids of *burchelli,* but other migrants tend to desert after a few minutes at the periphery.

The tendency of some migrants to stay at swarms of *praedator* and to wander in and then leave swarms of *burchelli* causes some difficulty in comparing relative numbers of migrants at swarms of the two species, especially since I usually watched swarms of *burchelli* longer than I watched swarms of *praedator.* Migrants probably favor swarms of *praedator* even more strongly than is indicated by Figure 1 and by tables throughout this report, since at any one time a greater percentage of the final total of migrants for a swarm would be actually present at a swarm of *praedator* than at a swarm of *burchelli.* However, the laborious calculation of the average number of birds present (minutes bird A was present plus minutes bird B was present, etc., divided by the minutes I watched at a given swarm) rather than use of final totals would only enhance, not detract from, the arguments in preceding paragraphs.

Resident Birds Leave Swarms of *Labidus praedator* to Migrants

Why should the dominant resident birds leave swarms of *L. praedator* to the migrants? Resident birds sometimes crowd into a nearby and previously unattended swarm of *praedator* and attend it for hours, if the swarm of



Squirrel Cuckoo (*Piaya cayana*). Painting by Don Richard Eckelberry.
Reproduced through the courtesy of Western Printing and Lithographing Company.

burchelli they were following suddenly stops raiding for one reason or another. At other times one finds many resident birds at a swarm of *praedator* even though a colony of *burchelli* is nearly unattended nearby. The reason resident birds favor *burchelli,* other than the larger average size of swarms and the tendency to flush larger insects, may be that raids of *burchelli* are easy to find and follow and regular in swarming. A given colony of this ant swarms on the surface every day for at least three weeks at a time, so that professional ant-followers can and do follow the same colony for three weeks, come back during or after a period of two weeks (the middle of the statary period), and attend the colony for another period of three weeks. The residents rarely can follow the unpredictable swarms of *praedator* for as many as five days in a row. *Praedator* swarms at night or underground some of the time and thus is very irregular about swarming above ground. Although colonies of *praedator* are two to six times as numerous as colonies of *burchelli,* one must search widely to find a colony of *praedator* each day but can follow a single colony or two of *burchelli* without much searching. Probably the birds have the same trouble the ornithologist has in finding swarms of *praedator* and, in addition, are subject to predation by the sit-and-wait hawks so prevalent in tropical forests.

Why Migrants Follow Swarms of *Labidus praedator*

However, the preceding argument does not explain why resident birds do not increase in numbers until they occupy all the swarms present. If the generalized migrants can locate swarms of *L. praedator,* what stops some generalized resident from doing so if Malthus and Darwin were correct about the natural increase of animal numbers? Possibly what I have elsewhere called the "irregularity principle" is involved: biological or physical irregularities in the environment create open niches or superabundances of food, because exploitation of a niche always lags behind its appearance. Irregularity can occur in time or space. The principle raises the possibility that superabundant food may be common rather than exceptional. At some times of year or irregularly, low points in availability restrict the populations of any exploiting species, so that at other times there is unused food which a migrant or similarly generalized species can exploit if it has alternate sources of food.

In tropical forests, resident and specialized species would find it particularly difficult to exploit seasonal or irregular peaks of food supply. Clutch sizes of tropical birds are small and reproductive rates low compared to clutches and reproductive rates of nontropical birds, perhaps because there are fewer hours of sunlight to feed young and poorer food supplies per species in the tropics (Lack, 1965). Predation commonly destroys 80 to 90 per cent of the nests in tropical forests, lowering reproductive rates directly and encouraging tropical birds to keep the number of young per brood low so parents will not have to visit so often (Skutch, 1949). It may even be undesirable from the point of view of survival of the species to set up a reproductive system which could exploit brief irregular peaks (see Wynne-Edwards, 1962) unless surplus birds can be instantly eliminated when poorer conditions return. When there are lows in abundance of food, there would be far more inter- and intraspecific competition and strife than is the case now. Probably the eventual population would be lower after a time of low numbers of swarms than would be the case if fewer birds had been present beforehand. There would be wild fluctuations in abundance rather than the fairly stable population which is probably the most efficient for use of a given resource when and where it occurs. In the tropics, where there are many species of predators on a species and many competitors for it, the fluctuations of populations might allow a competitor to take over. In simple environments, such as the Arctic, a species might be permitted to fluctuate if it has no competitors; it may even gain some benefit from fluctuations, which may make it hard for hawks and other higher carnivores to use as long as there are few species of predators and few alternate prey.

The argument that resident birds are limited by periodic low numbers of swarms and thus leave openings for migrants applies mainly to professional ant-followers. There are many resident "amateur" ant-followers which have other food supplies when ants are not available. Figure 2 indicates that some of the highest average numbers of resident birds were recorded in the very months when migrant birds were most numerous at swarms. The professional ant-followers account for only a minor part of the increase in resident birds. Since the resident amateur ant-followers generally dominate migrants on the few occasions when birds of the two groups compete directly, why do the resident amateurs not crowd the migrants away from swarms?

Why Resident Birds Do Not Crowd Migrants from Swarms

Variations of the irregularity principle may help explain why residents cannot take the food which migrants exploit. The resident amateurs, like the resident professionals, have low breeding rates. They are subject to high predation of nests.

Migrants, by contrast, have the high breeding rates characteristic of northern species. They can pour large numbers of individuals into situations which residents cannot safely occupy and still end up with enough survivors to replenish the stocks the next year. For instance, resident species are usually extremely jittery or hide while ants pass through very open woods or openings where there is no dense cover nearby. Migrants, by contrast, are very active and tame whether ants are passing dangerous areas or not. Hawks and other predators must take a tremendous toll of migrants, but a small number of survivors can still replenish stocks. If resident species were this oblivious to danger, they could not reproduce fast enough to make up the losses each year. Residents often cannot develop local migration patterns which would allow them to exploit seasonal or new food supplies in different areas, simply because the loss during migrations could not be made up during breeding seasons.

In many cases the niches occupied by resident amateurs at other seasons continue to be available or expand at the times of surpluses of swarms. The species are faced with the choice of continuing the kind of exploitation for which they are adapted or of temporarily changing to some extent their modes of exploitation. When the mode need not be changed very much, there is often an advantage for an amateur resident bird in moving to the cornucopia of arthropods flushed by swarms. If the mode of exploitation must be changed greatly, or if the resident amateur is subordinate to the professional species, the amateur is less likely to move in to the swarms even though food thus goes unexploited.

Exploitation of two or more foraging zones in a given area may often be more difficult than exploiting the same type of zone in different areas at different seasons. Some combinations of foraging zones simply cannot be exploited by a resident bird with a single morphology, although sexual and age differences in morphology and behavior assist some species; but these differences are limited in birds as compared with insects or even mammals.

As many authors have noted, the morphology and physiology of a generalized species are unlikely to fit well in all situations it could exploit, particularly if it must compete with the many specialists in the tropics. The same is true for mental physiology; time is also needed for evolutionary learning ("instinct") or for individual learning to allow a species to find different sources of food. The mental, physiological, and morphological conservatism of the amateur resident species must leave openings for migrants whenever ant swarms or any other sources of food increase briefly.

Since the resident species are unable to increase to meet the foraging opportunities at times of unusual abundance of swarms, the migrant species find openings even at swarms of *Eciton burchelli*. *Labidus praedator* swarms more irregularly from day to day and year to year than does *burchelli* and thus provides even more foraging opportunities for migrants (because of the irregularity principle) than do swarms of the latter.

The difference between 1960 and 1961 in swarm-following by autumnal migrants fits in with the hypothesis that these birds are exploiting irregular food supplies which resident birds cannot use. Data from the Operation Recovery Program, it has been noted, do not support the alternative hypotheses of a general drop in numbers of migrants between 1960 and 1961 or a shift of migration patterns. In the fall of 1960, an unusually wet year, there were many swarms of *praedator*. These swarms were generally poorly attended by resident birds. Migrants moving into the area probably found swarm-following an easy way to obtain food. Migrants also moved in to swarms of *burchelli* in late October, but the increasing numbers of resident birds at these swarms soon left little space for migratory birds. The latter continued to follow the poorly attended swarms of *praedator* well into early December. In 1961 the returning migrants attempted to move in to swarms of both species of ant, but in a year of normal rainfall the number of swarms of *praedator* was low. The migrants, soon excluded by resident birds, moved on to other food sources, perhaps to other parts of Panama where rainfall and numbers of swarms of *praedator* were locally unusually high in 1961. This hypothesis, which should be tested by further years of observation at various places in the Canal Zone, suggests that migrants move into areas where swarms of *praedator* are superabundant because of locally high rainfall or other factors. Observed differences in numbers of migrants from year to year would be due less to variations of wind patterns than to varying local movements to superabundant foods at stopover points.

The Role of Migrant Birds in Tropics Generally

The observations at swarms of ants thus suggest that the subordinate migrants use swarms only when the latter produce food surpluses which the dominant resident species cannot exploit. Is the role of migrant birds at swarms similar to the role of migrant birds in the tropics in general?

Morel and Bourliere (1962), in their study of migrants and residents on a savanna in Senegal, also concluded that migrants use "seasonal food surpluses that sedentary species are unable to exploit entirely." They attributed the preference of migrants for savannas and open country over forests in Senegal to the greater seasonal irregularity of the former habitats, which keeps numbers of resident species low or forces them to undertake local migration.

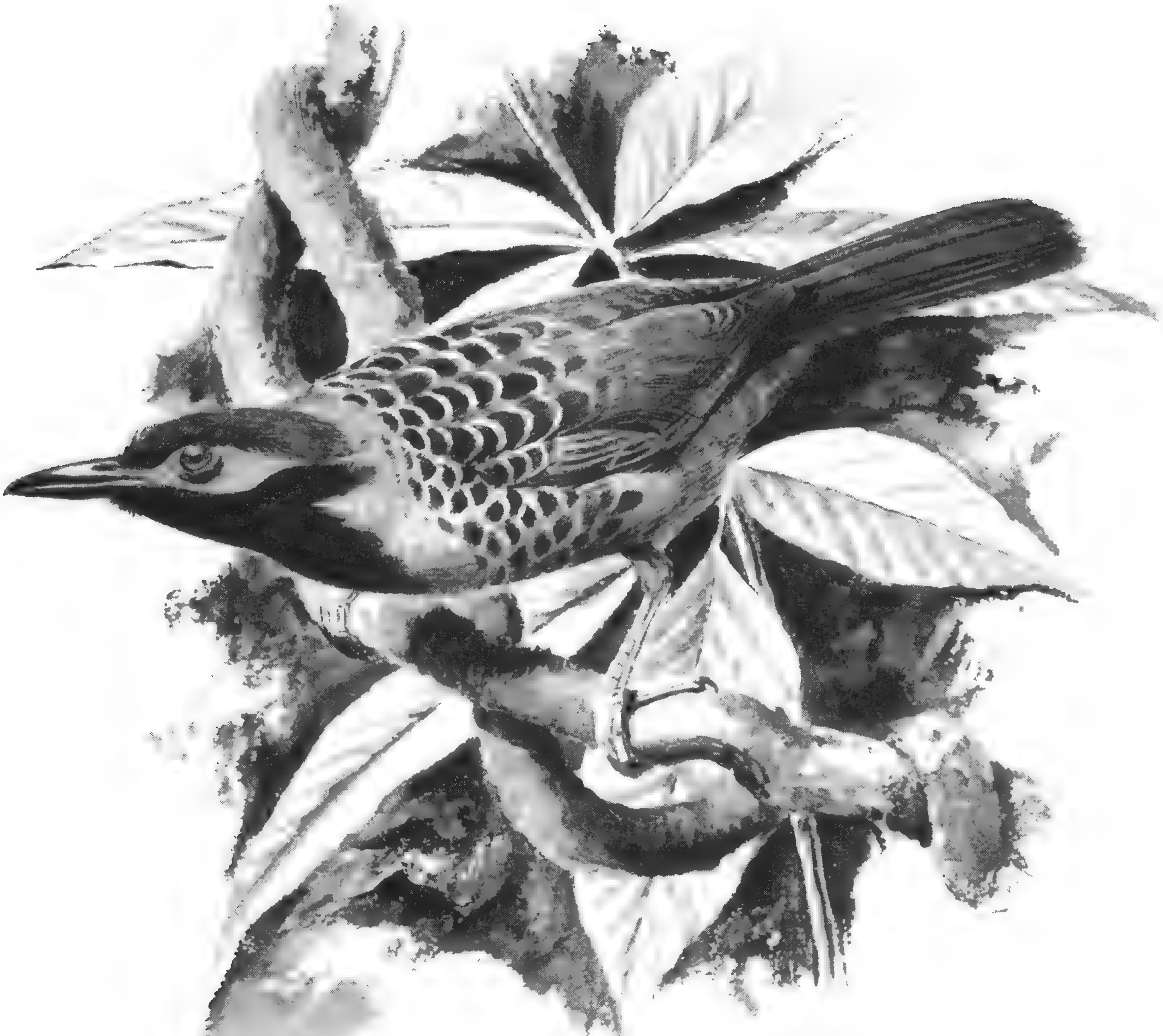
My observations of migrants in Central and South America agree with those of Morel and Bourliere in Africa. Migrants in the areas I have visited favor the environments which are irregular in time (bad seasons, new habitats, seasonally fruiting trees, etc.) or space (small, fragmented, or isolated habitats) and are thus likely to have irregular food surpluses unused by resident birds. Migrants are most common in highland areas, which are generally isolated islands of habitat where resident competitors are likely to be locally absent or at least rare. More particularly, migrants favor secondary successions, isolated patches of trees, and similarly disturbed areas where local species have not had time to move in or cannot do so because the available habitat is too small or too new a type. That forest-inhabiting migrants winter in the coastal strips of the West Indies and Central America or the montane strips of forest in the Andes suggests that they exploit the spatial irregularity of these strips of forest. The almost complete absence of forest or forest-edge migrants in Amazonian forests is very difficult to explain unless one supposes migrants exploit environmental irregularity. The nearly complete absence of migrants at El Tigre, in the perpetually wet forests of western Colombia, also supports this hypothesis. Observations in the Pacific and Amazonian forests should be extended over the whole year, of course. Since the irregularity principle predicts that resident professional species should replace resident amateur species in areas of greater environmental constancy, observations in such areas should prove valuable even if (as I suspect) migrants are so rare that it is difficult to observe them even at the peak of fall migration.

Do Migrant Birds Restrict Breeding Season of Residents?

Miller (1963), however, suggested that migrants may have a more dominant role than that of gleaners of irregularly timed or spaced surpluses. He proposed that migrants may restrict the breeding seasons of resident birds in the equatorial "cloud forest" where he worked at San Antonio, in the Cordillera Occidental of Colombia. This implies that migrant birds are actually competing with resident birds enough to take food the latter might use to rear young. Miller based his argument on the observations that migrants were common at San Antonio, forming 10 to 15 per cent of the individuals at certain seasons, and that fewer local species nest during the months when migrants are present.

I visited the slopes of the Cordillera Occidental near Miller's study area in March 1962 and can confirm that migrants are common there. This is exactly the sort of region where migrants should swarm if they are exploiting irregular habitats that provide superabundant foods. The day length varies little and rainfall varies only moderately in any one place, but in other respects these montane forests are very "irregular." They are narrow and thus provide rather small islands of habitat in seas of lowland forest. Tremendous differences in rainfall on the slopes of the Cordillera Occidental near San Antonio (West, 1957) decrease the sizes of patches of habitat even more. In such cases the number of resident species in a given habitat is always reduced (Preston, 1962). The fewer the resident species, the more food sources will be partly unexploited.

Moreover, the people of Colombia have been cutting and burning the montane forests at a dismaying rate. As they do so the native birds, except for a few very abundant open-country species, are disappearing incredibly fast. The patches of forest and second growth around San Antonio now support only a few of the species which once inhabited the slopes of the Andes in that region (Chapman, 1917). The difference between Miller's viewpoint and the viewpoint of Slud (1960), as mentioned in the introduction, is perhaps to be expected. Migrants are indeed far more numerous in the



Ocellated Anthrush, *Phaenostictus mcleannani*. Drawing by Arthur Singer.

variable and man-disturbed area where Miller worked than they are in continuous lowland forests anywhere in the tropics.

Still, the fact that migrants are abundant is no proof that they are using food needed by resident species. In late October of 1960 on Barro Colorado, 60 per cent of the birds at swarms of *Labidus praedator* were migrants. However, the resident antbirds were still breeding actively and successfully. They took whatever food they needed with little interference from the unasserting migrants. For these few months, there were just too many swarms about for the resident antbirds to occupy them completely.

The April and May peak of nesting at San Antonio was a second observation which led Miller to suspect that migrants may restrict the breeding of residents near San Antonio. However, this peak is much like that in adjacent areas of Central and northern South America (Snow and Snow, 1964), not a June to September peak as should be the case if residents are restricted by migrants. In some of these areas, such as Trinidad, migrant birds are much less numerous than at San Antonio. The reasons for a seasonal low in nesting in October to December must be climatic, probably affecting food supply and applying both to areas where migrants are numerous and to areas where migrants are scarce. Moreau (1952) points out that in Africa migrants north of the Equator arrive when local birds are not breeding, but migrants south of the Equator reach their maxima at the same time as resident birds are breeding. The same probably would apply in the New World but for the fact that few migrants go south of the Equator.

Morel and Bourliere (1962) mention that in Senegal a resident hoopoe nests at the time of year when the migrant species is absent. This specific case and similar ones, which may be discovered, are worth closer study since in some isolated cases migrants may restrict breeding seasons of residents. However, I predict that studies will indicate that the African hoopoe cannot breed when the migrant is present for some reason unconnected with competition from the migrant.

If the role of migrants is to use food supplies which resident species cannot use, the resident species must replace migrants whenever there are no new changes in an environment. Eventually resident species which are dominant to, better adapted than, or better acquainted with local conditions than the migrants should find some way of exploiting the irregular food supply which the migrant now uses. Residents should replace migrants first at the most constant end of the migration pattern, in this case in the tropics. Some environments, especially northern areas and savannas with long dry or winter seasons or extremely irregular conditions, may be so variable that resident species will replace migrants very slowly if at all. However, the extra mortality and morphological demands on a migratory species often will make resident species (perhaps mammals) superior as soon as some can find a way of staying the year around. The efficient use of a food source by a resident bird at one point along a migrant's route means that the migrant will have to find alternate food or disappear everywhere, even though food remains for it elsewhere along its course. Certainly migrants are very adaptable (or can move readily) and in some cases can turn to alternate food supplies to fill in the annual food pattern.

The preceding argument suggests the possibility that migrant populations may be limited not by competition on the nesting grounds but by competition from residents at more constant environments through which the migrants pass at other times of year. Lack (1965) thinks that the very high clutch sizes of northern birds may mean that not enough survive the winter to really use fully the extreme superabundance of food in the northern summer. The subordinate status of migrants at swarms of ants does suggest that there would be more thrushes and other birds in the north in summer if there had not been so many resident ant-followers at swarms in the tropics the preceding winter. Birds which are driven away must hunt for new sources of food and in the process expose themselves to predators and other hazards of search or local migration.

My own prejudice is to think that Lack is right in attributing population control in some migratory species to competition on the wintering grounds. However, I observed migrants in an unusually competitive tropical situation. Some migrant species may be limited in other ways than by competition in the tropical wintering grounds. Limitation of numbers on the breeding grounds or factors acting in late summer or during long migratory flights are two alternatives.

Are "Songbirds" Replacing the "Suboscines"?

The theory that migrants are adaptable—in the sense of moving readily from one superabundant food source to another—but are unable to compete directly with specialized resident species has some bearing on the viewpoint that "advanced" Old World passerines or "songbirds," such as thrushes, are gradually outcompeting and thus replacing antbirds and other "lower" passerines or "suboscines" in the Old and New Worlds (Mayr and Amadon, 1951). This viewpoint, generally if loosely held by "northern" ornithologists, derives in part from the replacement of South American fossil mammals by ones coming from the Old World via North America and in part from the comparative rarity of suboscines in the Old World.

Slud (1960) challenges this "conventional wisdom" with a convincing argument that the thrushes and other songbirds which have reached the New World do not replace the 1,100 species of antbirds and other suboscines, but instead take open and peripheral habitats while the suboscines dominate in the great tropical rain forest. In other words, the groups are adapted for different types of habitats and complement each other. The observation that migrant thrushes definitely do not exclude antbirds and other suboscines, but instead are subordinate to them and take foods no resident bird could use, supports and extends Slud's analysis. That migrant and resident songbirds in general use irregular habitats and superabundant foods rather than compete with suboscines also supports the viewpoint that the resident songbirds are not in the process of replacing the resident suboscines. Resident thrushes and other songbirds follow ants where, as in the highlands or on Trinidad, professional ant-followers (mostly suboscines) are few, perhaps because ants are rare or forests small or isolated.

In general, birds which we call the "advanced" songbirds are birds which are adapted to open, broken, montane, northern, or other peripheral habitats rather than to the forest. The "lower" birds with the biased name "suboscines" are mostly birds adapted to tropical forests. The division between the two groups is mainly based on the more complex syrinx of songbirds. Basing the classification on one morphological character raises the probability of polyphyletic origin of both groups, although similarity of syrinx may often show relationship. Evidence is accumulating that forest birds commonly use low-pitched and rather pure tones, perhaps because high-pitched sounds attenuate rapidly in the forest. Birds of the open are not so restricted. Forest birds, particularly tropical ones, live in fairly constant environments and may stay mated all year. Birds of open or peripheral habitats often mate for only part of the year, especially if they have to migrate. There is obvious selective pressure for complex songs and a complex syrinx in northern and open-country species which have temporary pair bonds, sing only at a time of year when other species are filling the air with sound, or must attract mates to tiny patches of habitat or to isolated nest-trees. If the complexity of the syrinx is adaptive, there is reason to suggest that the simple syringes of Old and New World "lower" passerines may have been evolved independently to fit them for life under the relatively constant and widespread conditions of tropical forests. There is no reason to think that complex syringes have been derived from simple ones and never the reverse; the trend in the vertebrate skull, for instance, has been toward reduction in the complexity of bones. Possibly the tendency of ornithologists to consider thrushes and other songbirds as more "highly evolved" and hence "superior" to suboscine birds derives from the fact that man associates more often with birds having complex syringes, since both he and they are adapted to open habitats or secondary successions rather than to the depths of forests. We naturally tend to place birds with which we are familiar higher than birds which are strange to us when we have no independent criterion for judging the direction of evolution. Then we assume that, because they are superior in song, they are superior in other respects.

In fact, this study shows that the reverse is likely to be true when songbirds and antbirds do compete. I think one could state that suboscines often replace songbirds by direct competition, but songbirds replace suboscines only when the habitat has been changed so that the suboscines would disappear anyway. The statement may be valid a greater percentage of the time, however, when resident species replace migrants or *vice versa*.

Alden H. Miller and John Terborgh, who have worked in tropical forests of the New World, told me that the forest interior in New Guinea is extremely poor in bird species compared to the forest interior in Central and South America. If the depauperate forests of New Guinea are typical of forests of the Old World, perhaps passerines with simple syringes could be expanding there. Antbirds and woodcreepers, if they could spread to tropical forests in the Old World, probably would find many open niches or displace Old World thrushes which casually exploit the foraging opportunities left by the relative absence of birds really adapted to tropical forests. Of course, the relative absence of passerines with simple syringes in the Old World may reflect the relatively limited extent and isolation of tropical forests there. If so, there may be relatively little room for species requiring constant conditions.

Man's Effect on Relationship Between Songbirds and Suboscines

Man is changing the whole competitive relationship between the suboscines and songbirds, between migrants and antbirds. As he cuts the tropical forest into small pieces, he creates irregular environmental conditions which eliminate native species, particularly suboscines, and provide for a time new opportunities for resident or migrant birds of open or peripheral habitats. At the same time, he is eliminating some of their habitats in the north by building cities, roads, "clean" farms, and the like. Besides the obvious and catastrophic decline in numbers of forest-adapted resident birds in the tropics, I am uncertain what the net effect has been. Perhaps many migrants are temporarily increasing in numbers as they use the surplus foods made available by the extinction of local species and by rapid environmental changes. Resident birds of open and edge habitats certainly increase temporarily as the wave of cutting and burning breaks up the original forest. The eventual result, as the forests disappear completely, will be disappearance of migrant as well as resident species, except for a few birds which man will probably consider pests because they are too well adapted to opportunities he provides. That suboscines will predominate among the extinct species will not, however, prove that they were inferior to the remaining few songbirds when conditions were less disturbed by man. This study should show that the suboscines here considered were a dominant and well adapted group, not a scattering of relicts which migrants and other songbirds would have eliminated anyway if man had not done so.

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Summary

Despite frequent supplantings and high competition for space among resident birds which follow swarms of army ants, several migrants from North America follow the ants in the tropics. On Barro Colorado Island in the Panama Canal Zone such wintering species as Acadian Flycatchers, Wood Thrushes, and Kentucky Warblers commonly follow ants. In the fall migrations of 1960 and 1961, many other migrants crowded in at the swarms, especially Swainson's Thrushes, Gray-cheeked Thrushes, Veeries, and Canada Warblers. In the spring migration, 1961, few species followed swarms. Other migrant species, among them ground-foraging warblers of the genus *Seiurus,* generally ignore ants.

At Gallon Jug, British Honduras, the wintering Hooded Warbler also follows army ants. It seems to be rare in areas where the resident Spotted Antbird follows swarms and forages in a rather similar fashion. Wood Thrushes seem to be absent at various places in the Canal Zone where the similarly foraging resident, the Black-faced Antthrush, follows swarms. Competitive exclusion may play a part in these patterns of distribution.

Foraging behaviors of the migrant and resident birds tend to differ. Wintering species generally have niches quite different from those of resident birds and seldom approach them. Migrating species also differ in their niches from resident birds, but migrant thrushes also crowd in near the centers of swarms and compete directly with resident birds at times of high abundance of migrants. The thrushes and other migratory or wintering species are virtually always subordinate to resident birds, which chase them away and expend very little energy doing so. The migrants are thus restricted to the periphery of swarms, in poorer areas for foraging, whenever resident species are present. The resident species definitely restrict the roles of migrant species and exclude them from swarms whenever competition could occur. There is no evidence for restriction of resident birds by the unassertive migrants.

Competition between migrant species was not noted often. Migrating individuals generally tolerate others. Wood Thrushes dominate Swainson's Thrushes, which dominate Gray-cheeked Thrushes and the retiring Veeries. Wintering individuals generally seem to be territorial, for they drive off other members of their own species.

Whereas resident birds crowd in to the large and regular swarms of the army ant *Eciton burchelli,* migratory birds are more frequent at the smaller and infrequent swarms of *Labidus praedator.* In the fall of 1960, heavy rains resulted in very high numbers of swarms of *praedator* since it swarms above ground mainly in wet weather. Migratory birds, especially thrushes, flocked to swarms in October and November to a far greater degree than they did in the fall of 1961. In that year normal rainfall led to rather low numbers of swarms of *praedator* and migrants were nearly absent in November.

The peripheral positions of migrants and their tendencies to follow the unpredictable swarms of *praedator* suggest that they are excluded by resident species whenever food is not superabundant. The migrants thus seem to use what may be called the "irregularity principle," that the exploitation of a niche (in this case by resident birds) must lag behind the appearance of the niche. The principle and the subordinate status of migratory birds seem

to account for many of the seasonal and species changes at swarms on Barro Colorado. It is somewhat surprising to find that the tropical forest is inconstant enough to provide niches for the migrants, especially at swarms of army ants. Possibly fluctuations in numbers and roles of migrants generally are explained by the theory that migrants depend on sources of food which cannot be exploited by local populations. If so, there should be local shifts of birds from areas with normal sources of food to ones with superabundant sources at stopover points on migration and in winter.

Observations support the theory that in Africa (Morel and Bourliere, 1962) and in the American tropics migrants avoid extensive tropical forests and favor "irregular" habitats, such as montane or isolated areas and areas disturbed by man. From these observations, the observations at swarms, and other evidence, there is reason to doubt Miller's hypothesis (1963) that migrant birds restrict the breeding seasons of resident birds in a cloud forest in Colombia. There is equally strong reason to doubt Mayr's and Amadon's contention (1951) that "songbirds" (including most of the migrants) are replacing "suboscines" (such as the antbirds at swarms) in neotropical regions. Instead, the simple syringes of "suboscines" may be adapted for vocalizations needed in forested habitats and under regular conditions, while the complex syringes of "songbirds" are adaptations for irregular breeding conditions and peripheral habitats. Both the "songbirds" and "suboscines" may be polyphyletic. Suboscines of the Old and New Worlds are especially likely to have arisen separately if simple syringes are adaptations for forest environments. Probably the present destruction of the tropical forests by man will exterminate more suboscines than songbirds, but this study indicates that the dominant and well-adapted suboscines would not have been eliminated by the songbirds had man not come along. Instead, they restrict the songbirds, especially the migrants, to the use of superabundant foods which resident species, mostly suboscines, cannot yet exploit.

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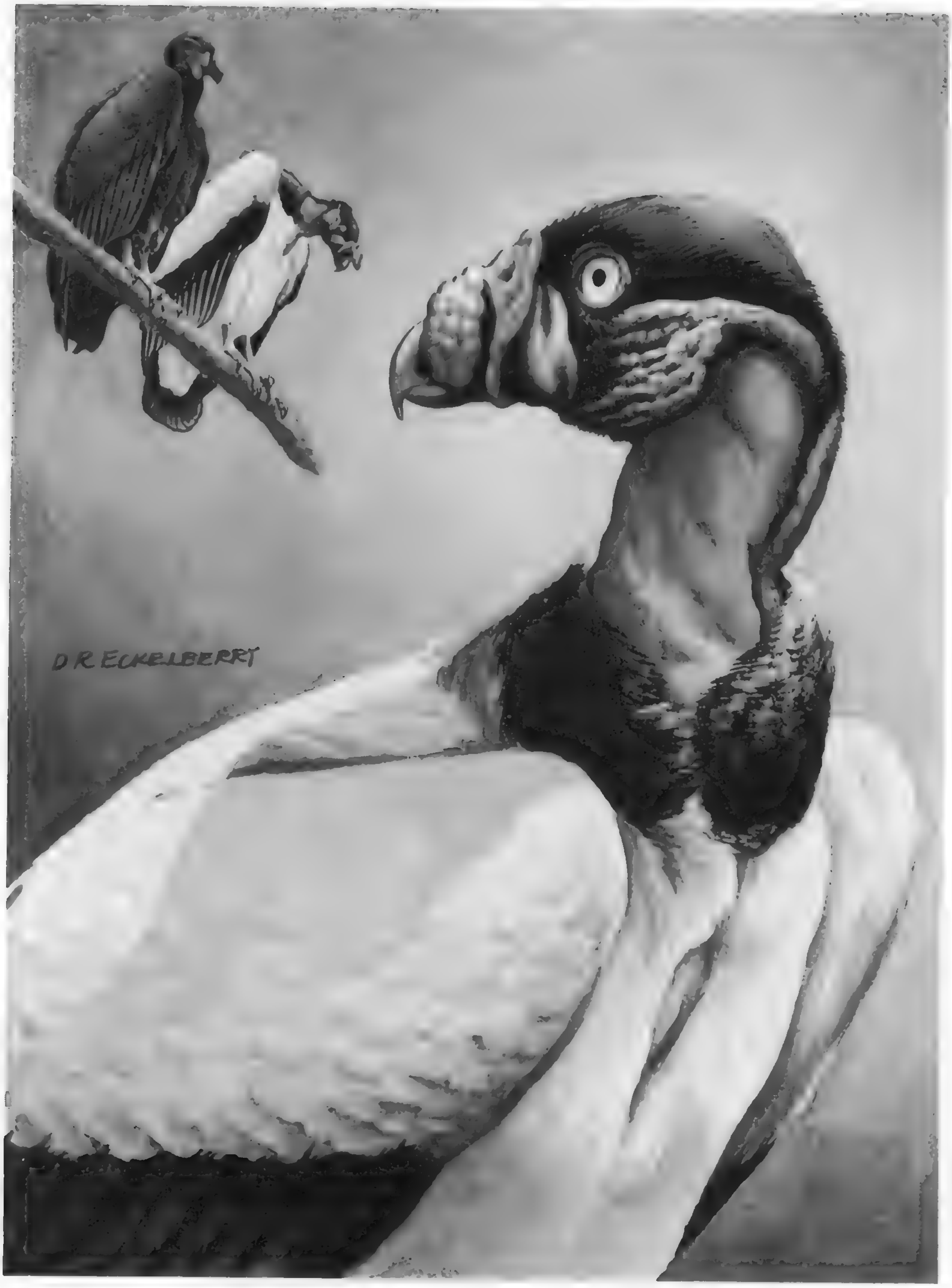

D R ECKELBERRY

King Vulture, *Sarcoramphus papa*. Painting by Don Richard Eckelberry.

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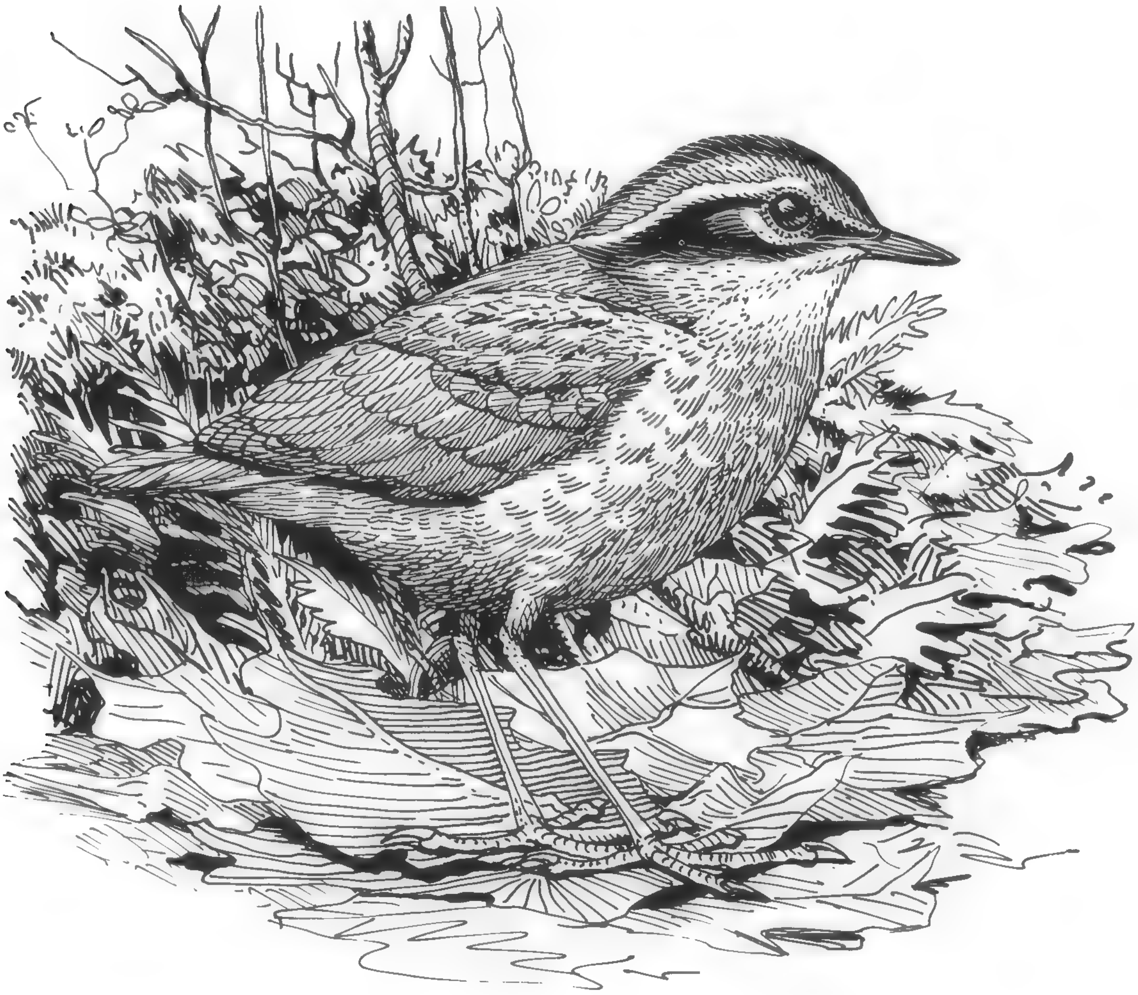

Indian Pitta, *Pitta brachyura*.

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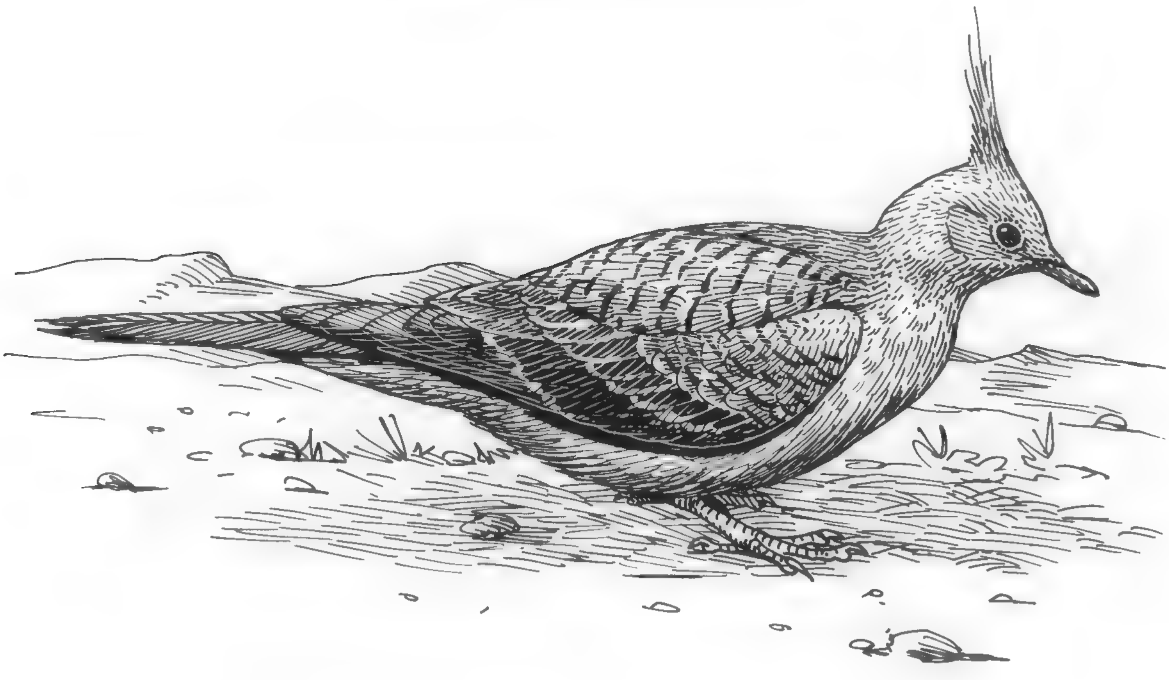

Crested Bronze-winged Pigeon, *Ocyphaps lophotes*

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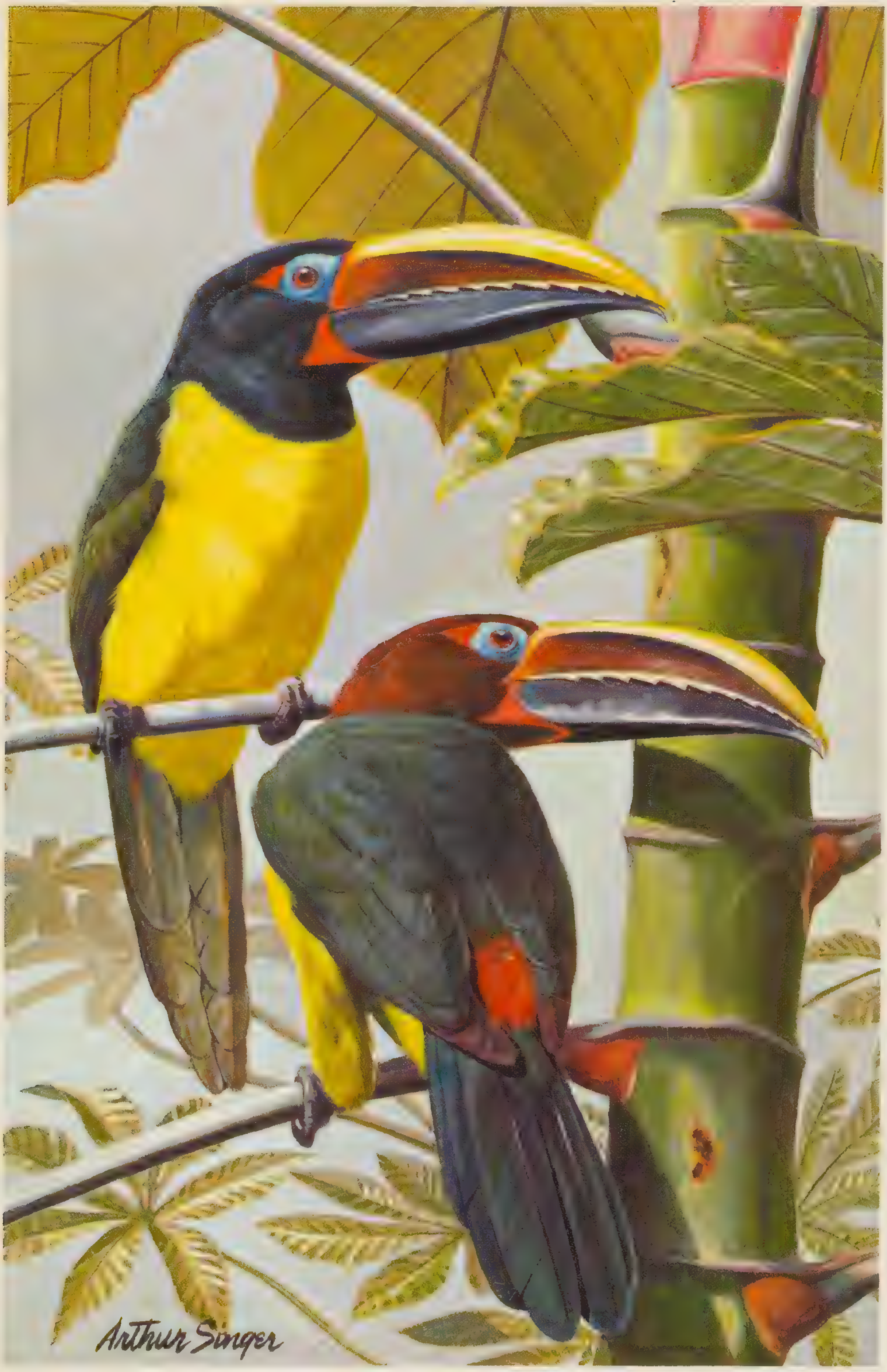
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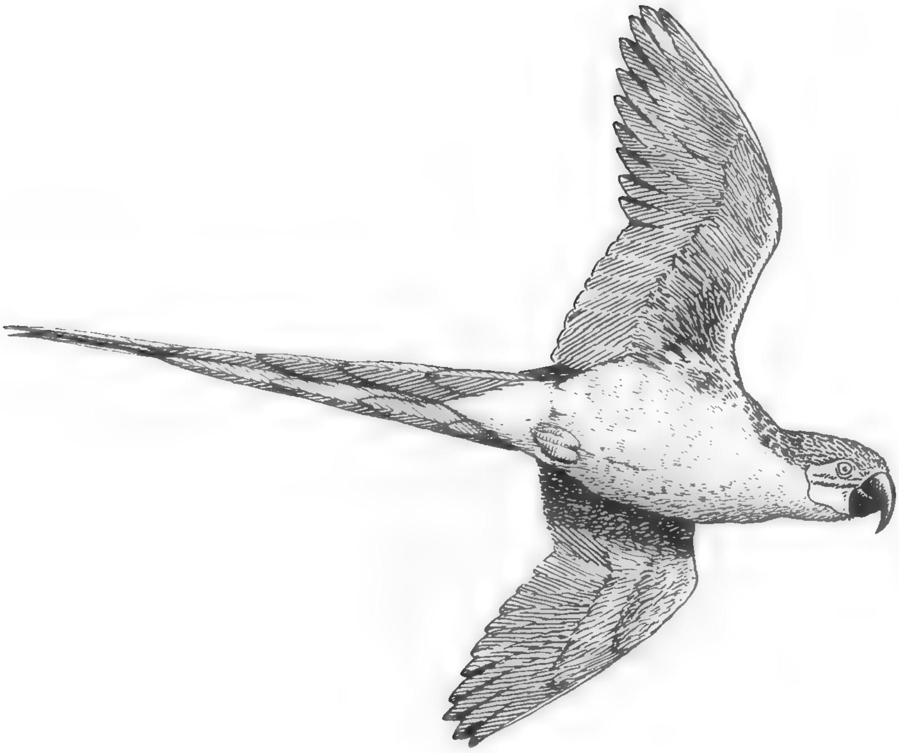

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CONTENTS

COURTSHIP BEHAVIOR IN MANAKINS (PIPRIDAE): A REVIEW. *Helmut Sick* . 5

OBSERVATIONS ON GALÁPAGOS TOOL-USING FINCHES IN CAPTIVITY. *George C. Millikan* and *Robert I. Bowman* 23

ECOLOGICAL AND BEHAVIORAL ASPECTS OF PREDATION BY THE NORTHERN SHRIKE. *Tom J. Cade* 43

FACTORS AFFECTING THE OCCURRENCE OF THE EURASIAN LAPWING IN EASTERN NORTH AMERICA. *Aaron M. Bagg* 87

THE DICKCISSEL ON ITS WINTERING GROUNDS IN TRINIDAD. *Richard P. ffrench* 123

SONGS OF THE YELLOWTHROAT. *Donald J. Borror* 141

THE STATUS OF NEWELL'S RACE OF THE MANX SHEARWATER. *Warren B. King* and *Patrick J. Gould* 163

ECOLOGICAL ADAPTATIONS IN THE LIFE HISTORY OF THE BROWN BOOBY AT ASCENSION ISLAND. *K. E. L. Simmons* 187

MIGRATORY FLIGHTS OF *Hylocichla* THRUSHES IN SPRING: A RADIOTELEMETRY STUDY. *W. W. Cochran, G. G. Montgomery,* and *R. R. Graber* 213

EGG-CARRYING BY THE PILEATED WOODPECKER. *Frederick K. Truslow* . . 227

COVER PAINTING OF THE GREEN ARACARI. *Arthur Singer* 237

THE AUTHORS AND ARTISTS BRIEFLY NOTED 239

STAFF, ADMINISTRATIVE BOARD, FACULTY AFFILIATES, RESEARCH COLLABORATORS, AND FIELD COLLABORATORS OF THE CORNELL LABORATORY OF ORNITHOLOGY, 1966-1967 241

MEMBERS OF THE LABORATORY OF ORNITHOLOGY, 1967 243

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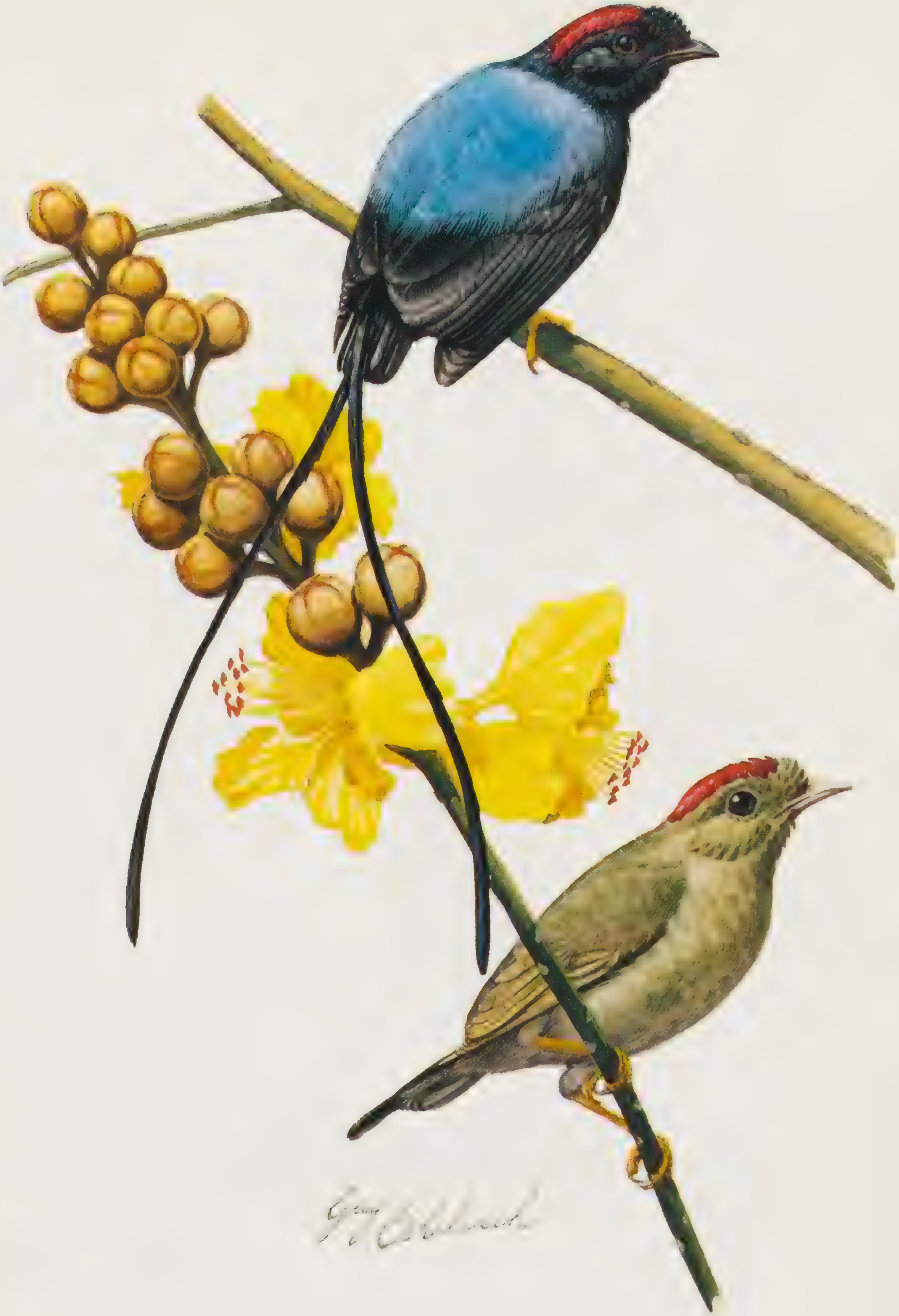

Long-tailed Manakin, *Chiroxiphia linearis.*
Male above, female below. Painting by Guy Cohleach.

COURTSHIP BEHAVIOR IN THE MANAKINS (PIPRIDAE): A REVIEW

HELMUT SICK

Manakins are among the most colorful small passerine birds of the Neotropics. Ranging from central Mexico to northern Argentina, the family Pipridae contains about 52 species (de Schauensee, 1966). The manakins dwell in the undergrowth and in the lower canopy. Because they do not leave the shadows of the forest, the broad rivers of Amazonia function effectively as barriers to their dispersal, accounting for the speciation of several populations isolated by rivers. Some species range widely throughout most of Amazonia. Others are more restricted. The distribution of the Blue-crowned Manakin (*Pipra coronata*) extends from Costa Rica and Panama southward throughout the tropical zone of Amazonian Venezuela, Colombia, Peru, northern Bolivia, and Brazil east to the Rivers Negro and Madeira. The Golden-crowned Manakin (*Pipra vilasboasi*) was only recently discovered (Sick, 1959c) in its restricted range between the Xingu and Tapajos Rivers in the state of Para, Brazil.

Among the most typical representatives of the family are the genera *Pipra, Chiroxiphia,* and *Manacus.* The males are gaudily clad, the females soberly greenish. The embellishments of manakins are often concentrated on the head: brilliant color (most species), stiffened frontal plumes (Helmeted Manakin, *Antilophia galeata*; Golden-winged Manakin, *Masius chrysopterus*; and Pin-tailed Manakin, *Ilicura militaris*), erectile feather horns (Scarlet-horned Manakin, *Pipra cornuta,* and Blue-backed Manakin, *Chiroxiphia pareola*), and opalescent crown feathers (Opal-crowned Manakin, *Pipra iris*). The irises are frequently white or red.

In one species the female sports a plumage almost as attractive as that of males (Striped Manakin, *Machaeropterus regulus*). In several species, including the Crimson-hooded Manakin (*Pipra aureola*) and Golden-headed Manakin (*Pipra erythrocephala*), cock-feathered females sometimes occur. In two genera (*Neopelma* and *Tyranneutes*) both male and female are a modest leaf-green in color. They wear a crest that is sometimes lined with yellow, reminding one strongly of such tyrant flycatchers as the elaenias (*Myiopagis*).

In some species the tarsal feathering is more extensive in the male, augmenting the visual effect of brightly colored thighs, as in the Red-capped Manakin (*Pipra mentalis*) in which the bright yellow thighs contrast sharply with the black underparts. The male Golden-headed Manakin averages a little smaller than the female, size probably functioning here for greater agility in flight during display (Snow, 1962b). *Manacus* exhibits very strong, brightly colored feet for its powerful jumping display.

The simple, cup-shaped nest built by manakins rests snugly in a low, horizontal fork, and is often so transparent that mosquitoes can suck the sparsely downed nestlings from below. In the Wire-tailed Manakin (*Teleonema filicauda*) and several others an excess of nest material hangs loosely below the hammock, rendering a cryptic effect to the nest. In some species, the nests may be only a few meters apart—eventually shifting to colonial grouping—and are often made near, or even over, the water. The female alone builds the nest. After depositing her two mottled eggs, she incubates them and cares for the young. The males, as far as known, do not participate in any of the duties involving the nest or the young. The emancipated males remain on or near their courts, where they engage in courtship "dances" and displays.

Manakins gather their food by side-stepping along branches to capture small invertebrates, or by fluttering to pluck berries or catch insects. The Helmeted Manakin ascends into the canopy of swamp forests, whereas *Manacus* may go to the ground to display.

Systematically, the Pipridae are customarily placed between the cotingas (Cotingidae) and the tyrant flycatchers (Tyrannidae) in the hierarchy, for they share characters of both families. One character of dubious value, tarsal scutellation, is shared by the Pipridae and Tyrannidae (Rand, 1959; Ridgway, 1907). The manakins share with the cotingas characters involving the syrinx (Müller, 1847) and thigh arteries (Garrod, 1876). Lowe (1942) studied the anatomy of the Golden-collared Manakin (*Manacus vitellinus*) emphasizing its function in display. Intergeneric hybrids among the Pipridae have been reviewed by Parkes (1961). The genera *Schiffornis, Piprites,* and *Sapayoa* appear to show more affinities with cotingas than with the Pipridae.

Now that the reader has been introduced to the manakins, I shall devote the remainder of this paper to the courtship behavior of the Pipridae and provide a comparative review of the various types of displays not yet undertaken in this manner by other ornithologists. I list below the 31 species of manakins that I shall mention. The common names are taken from de Schauensee (1966).

Crimson-hooded Manakin, *Pipra aureola*
Band-tailed Manakin, *P. fasciicauda*
Golden-headed Manakin, *P. erythrocephala*
Red-capped Manakin, *P. mentalis*
Scarlet-horned Manakin, *P. cornuta*
Blue-crowned Manakin, *P. coronata*
Opal-crowned Manakin, *P. iris*
Snow-capped Manakin, *P. nattereri*
Golden-crowned Manakin, *P. vilasboasi*

Wire-tailed Manakin, *Teleonema filicauda*

Helmeted Manakin, *Antilophia galeata*

Long-tailed Manakin, *Chiroxiphia linearis*
Lance-tailed Manakin, *C. lanceolata*
Blue-backed Manakin, *C. pareola*
Swallow-tailed Manakin, *C. caudata*

Golden-winged Manakin, *Masius chrysopterus*

Pin-tailed Manakin, *Ilicura militaris*

White-throated Manakin, *Corapipo gutturalis*
White-ruffed Manakin, *C. leucorrhoa*

White-bearded Manakin, *Manacus manacus*
Golden-collared Manakin, *M. vitellinus*

Fiery-capped Manakin, *Machaeropterus pyrocephalus*
Striped Manakin, *M. regulus*

Club-winged Manakin, *Allocotopterus deliciosus*

Black Manakin, *Xenopipo atronitens*

Flame-crowned Manakin, *Heterocercus linteatus*

Wied's Tyrant-Manakin, *Neopelma aurifrons*
Saffron-crested Tyrant-Manakin, *N. chrysocephalum*
Pale-bellied Tyrant-Manakin, *N. pallescens*

Tiny Tyrant-Manakin, *Tyranneutes virescens*
Dwarf Tyrant-Manakin, *T. stolzmanni*

Methods

The ideal methods for analyzing the displays of manakins include tape recordings and movie film. For many species, however, these techniques are difficult to apply, because the forest interior is unsuitable for photography, the birds often perform at some distance up in the trees, and the relative inaccessibility of many manakins makes the transportation of equipment impractical. Nevertheless, Snow (1962a and 1962b) succeeded in using these techniques to some extent. Most of the recorded information on manakin displays is direct observation.

The collection of data on the full range of courtship display in each species requires years of observation. Some species show a confusing diversity of behavior. The diversity may manifest itself among different populations (e.g., in the Pale-bellied Tyrant-Manakin, *Neopelma pallescens*), making it important to observe each species whenever possible in various parts of its range. Contradictions between authors generally are due to incomplete observations and may result in conclusions like those of Slud (1957) regarding the display of the Long-tailed Manakin (*Chiroxiphia linearis*): "Much of what I saw was obviously different from what others had seen. Much that others had seen was never observed by me." Language barriers undoubtedly complicate the contradictory observations on manakin displays.

Components of Manakin Displays

The manakins are especially noted for their courtship behavior. Each species has its own set of stereotyped elements which make up its typical display. Frequently, we can recognize the same ritualized elements in different species, an indication of its homology or evolutionary derivation. Such movements and postures include chasing, crouching, vibrating, tripping, side-to-side-sliding, pivoting, wing-raising, simple jumping, jumping upward with fluttering wings, flight displays to the perch, turning to face the direction from which it flew to the perch, snapping, and others.

Among the auditory signals, the advertising or invitation call of the male is especially important, since it serves to attract the attention of females and other males of the same species. In "solitary" species, such as the Dwarf Tyrant-Manakin (*Tyranneutes stolzmanni*), the advertising call is merely the unique expression of the male's readiness to mate. In the truly dancing species, the advertising call ceases when dancing begins. The advertising call of *Ilicura* resembles the location call of fledgling Swallow-tailed Manakins (*Chiroxiphia caudata*).

Mechanical Sounds

Manakins lack complex vocal repertoires. They lose vocal sounds in favor of the production of mechanical sounds, indicating that such sounds represent the more advanced evolutionary condition. Many species supplement the movements and postures of courtship with mechanical sounds. The evolution of this trait culminated in the unique transformation of several secondaries in the genera *Machaeropterus* and *Allocotopterus*.

Mechanical sounds may figure importantly in the displays of *Manacus*. But the wing-snapping is caused by secondaries only slightly modified in immature *Manacus* males with green plumage. And in *Neopelma* the sounds, caused by the violent closing of the wings, result from no structural modifications. The whirring sound produced by the primaries of *Chiroxiphia, Ilicura,* and *Manacus* is only heard in normal level flight, not on the court. In *Ilicura* the flight sound is not automatically produced.

The Band-tailed Manakin (*Pipra fasciicauda*) and *Manacus* land on a branch with a loud stamp during courtship. Manakins which use the tail to produce sound show a progressive shortening and stiffening of the rectrices. For this reason the male Band-tailed Manakin possesses a shorter tail than the female. The wire-like structure on the tail of *Teleonema* seem to be strictly ornamental.

Display Grounds and Their Function

Manakins gather on traditional dancing grounds which they occupy for decades if man does not disturb them. These places must meet the special requirements of each species: twigs that are firm, thin, horizontal or vertical and without side-branches and leaves; twigs that are at a certain height and other corresponding twigs at certain distances from each other; a clear approach to allow the display flight without obstacles. *Corapipo* and *Ilicura* need a horizontal log. Some species use slender limbs which move and shake their leaves when the bird perches on them. The moving foliage acts as an accessory to the display (Band-tailed Manakin and Pale-bellied Tyrant-Manakin). *Manacus* cleans its court, carrying away fallen debris. Some *Pipra* pluck leaves around them on the display branches. Such activities recall similar behavior by certain birds-of-paradise that strip off leaves above the arena, allowing well lighted perches that enhance their remarkable plumage. Gilliard (1959) proposed that the clearing of leaves off the ground and branches at the court serves as a defense mechanism that makes it difficult for predators to lurk on or near the court.

The display grounds are frequently within sound of each other (*Pipra*) and sometimes within sight (*Manacus*). The grouping of such courts (sometimes consisting of a single perch) in a limited arena enhances the excitement of the dancing birds. In *Manacus* this mutual stimulation results in bursts of display during certain hours of the day. Snow (1963b) stated that in several species of manakins the males may spend 80 to 90 per cent of the daylight hours on or near their display perches. In *Manacus* and *Pipra erythrocephala* males "own" their courting stage. In the Swallow-tailed Manakin, on the other hand, the court "belongs" to the whole group of interacting males, or to a dominant male in the group. One group of males of a species usually does not mingle with neighboring groups.

Displays of Manakins: Comparative Review and Evolution

Eight years ago I analyzed the display movements (numbering about 50) of 15 species of manakins that I observed in Brazil (Sick, 1959a). By now the courtship behavior of at least 25 species, or one-half the number of manakins, has been reported. The observations on many species are still fragmentary. Chapman (1935) made the first detailed study of manakin courtship behavior with his observations of the Golden-collared Manakin. Skutch (1949) worked with the Red-capped Manakin (also called the Yellow-thighed Manakin).

The diverse displays of the different manakins challenge an evolutionary treatment (Sick, 1959a and b, 1960; Snow, 1963b). There is no clear sequence from simple to complicated types of performances because the evolution of displays in Pipridae proceeds in different directions. It appears as though the acquisition of visual signal characters, such as specialization of plumage and structure, sometimes followed the evolution of exaggerated display movements. These movements involve the exhibition of certain parts of the body—rump, wings, and tail—that have not yet become especially ornamented.

Some manakins display solitarily, others in interacting groups. The solitary performance occurs in *Neopelma,* sometimes in *Pipra,* and in the main display of *Manacus.* The other type of display in which several birds dance together is achieved in two degrees: (1) dancing of two males together, as practiced by some *Pipra* and *Machaeropterus*; (2) gathering of three or more interacting males in a true communal display (*Chiroxiphia*).

Having evolved in different ways, one can consider the culmination of courtship evolution in the Pipridae as represented by the unique acoustic, solo display of *Manacus,* the unusual morphology of the remiges in *Machaeropterus,* or the fully synchronized performances of several males in *Chiroxiphia.*

Antilophia, Xenopipo, Heterocercus

Male Black Manakins (*Xenopipo atronitens*) and Helmeted Manakins (*Antilophia galeata*) show only a moderate development of courtship display that involves chases between males giving loud calls—true vocalization, not mechanical sounds. The males of these monotypic genera are black. The Helmeted Manakin has a crested, scarlet cap. Its call is noisy, sonorous, and varied, rather different from other manakins, but similar to some cotingas. The large, tyrant-like Flame-crowned Manakin (*Heterocercus linteatus*) behaves in similar fashion. The male of this species, when rendering its advertising call, spreads a white throat-patch laterally to form a compact "moustache."

Tyranneutes

The small, all-green Dwarf Tyrant-Manakin (*Tyranneutes stolzmanni*) displays vocally and solitarily. It advertises weakly, but tirelessly, from several twigs within a small area. Somewhat more elaborately, the Tiny Tyrant-Manakin (*T. virescens*) displays with a head-swinging performance and raised crest (the male has some yellow on the crown), and also with slow, floating flights with upright body (Snow, 1961).

Neopelma

From the displays of *Tyranneutes* it is but a step to the courtship of *Neopelma,* another genus with all-green birds. These piprids show different evolutionary stages of a more elaborate courtship display. Wied's Tyrant-Manakin (*N. aurifrons*) limits its display to a weak call. But the Pale-bellied

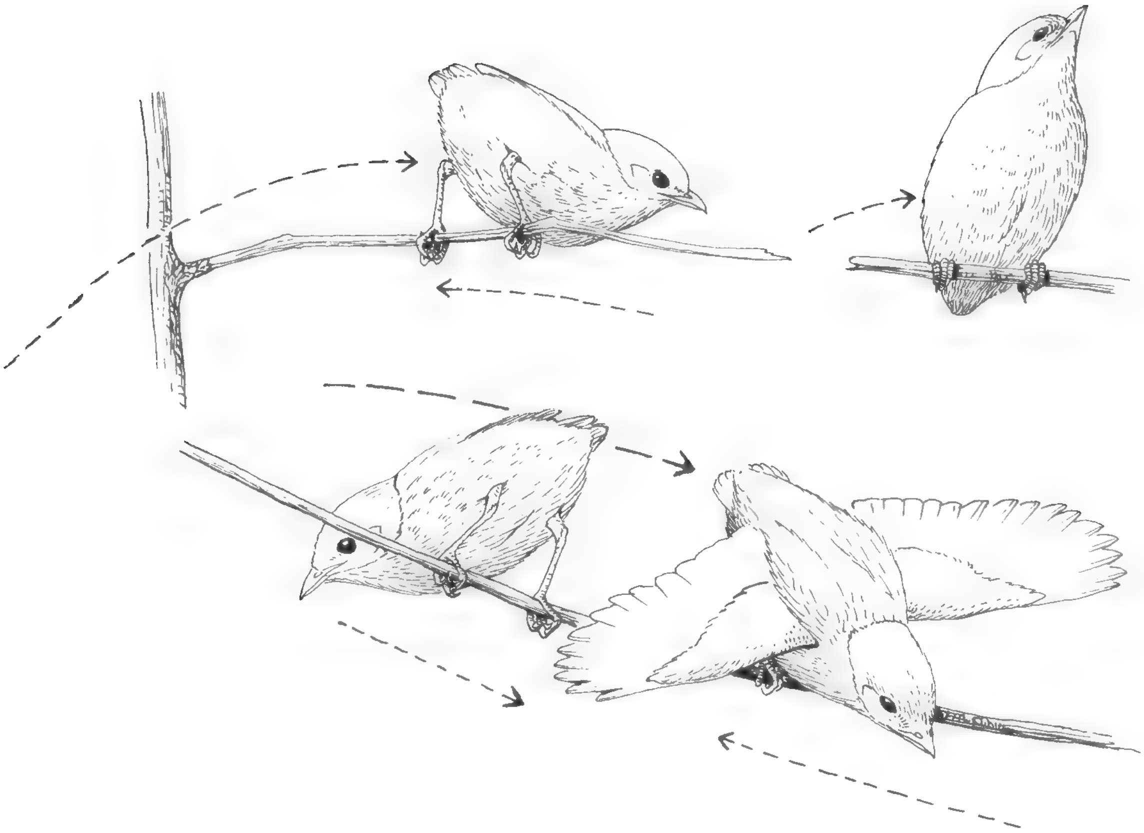

Figure 1. Courtship display of the Golden-headed Manakin, *Pipra erythrocephala rubrocapilla.* Above left, an adult male performing alone; above right, an adult male in an upright posture about to display; below, two adult males performing together, but not facing each other.

and Saffron-crested Tyrant-Manakins (*N. pallescens* and *N. chrysocephalum*) perform an upward jump and spread a yellow crest. In addition, *N. pallescens* produces a *dop-dop* sound during the jump by beating the wings together—not by special feather structure. Certain populations omit the wing sound (Sick, 1959a).

Pipra

The Golden-headed Manakin (*P. erythrocephala rubrocapilla*) has a highly complex courtship display (Figure 1 and Plate 1). The male lands on a thin twig about three meters high and calls *zlit.* He assumes an upright posture, sleeks the plumage, and quivers his tail. Then he makes short, straight flights between the twig on which he landed (main perch) and one or two nearby perches. Each time the male lands, he turns about to face the direction from which he has flown, and often calls a sharp *zlit* or *zi-gä.* With mounting excitement he crouches, holding the body at an angle of about 45 degrees to the perch and slides backwards with very short, quick steps, quivers the tail and wings, spreads the wings horizontally and closes them, or flicks the wings, uttering a long *siiiiiü-gäh.* Eventually, a female lands silently close besides the male and faces him. The male now slides still more quickly back and forth, always with his tail toward the female (conflict between fear and aggression). The male exhibits his red thighs, especially the one turned toward the female. He pivots frequently. The male maintains a critical distance from the female. Suddenly the male flies off on his display flight. He darts away about 40 meters and returns immediately in an extremely rapid swoop, describing an S-curve in front of the female, then tries to land on her to copulate. If she does not accept him, the male lands at her side with wings

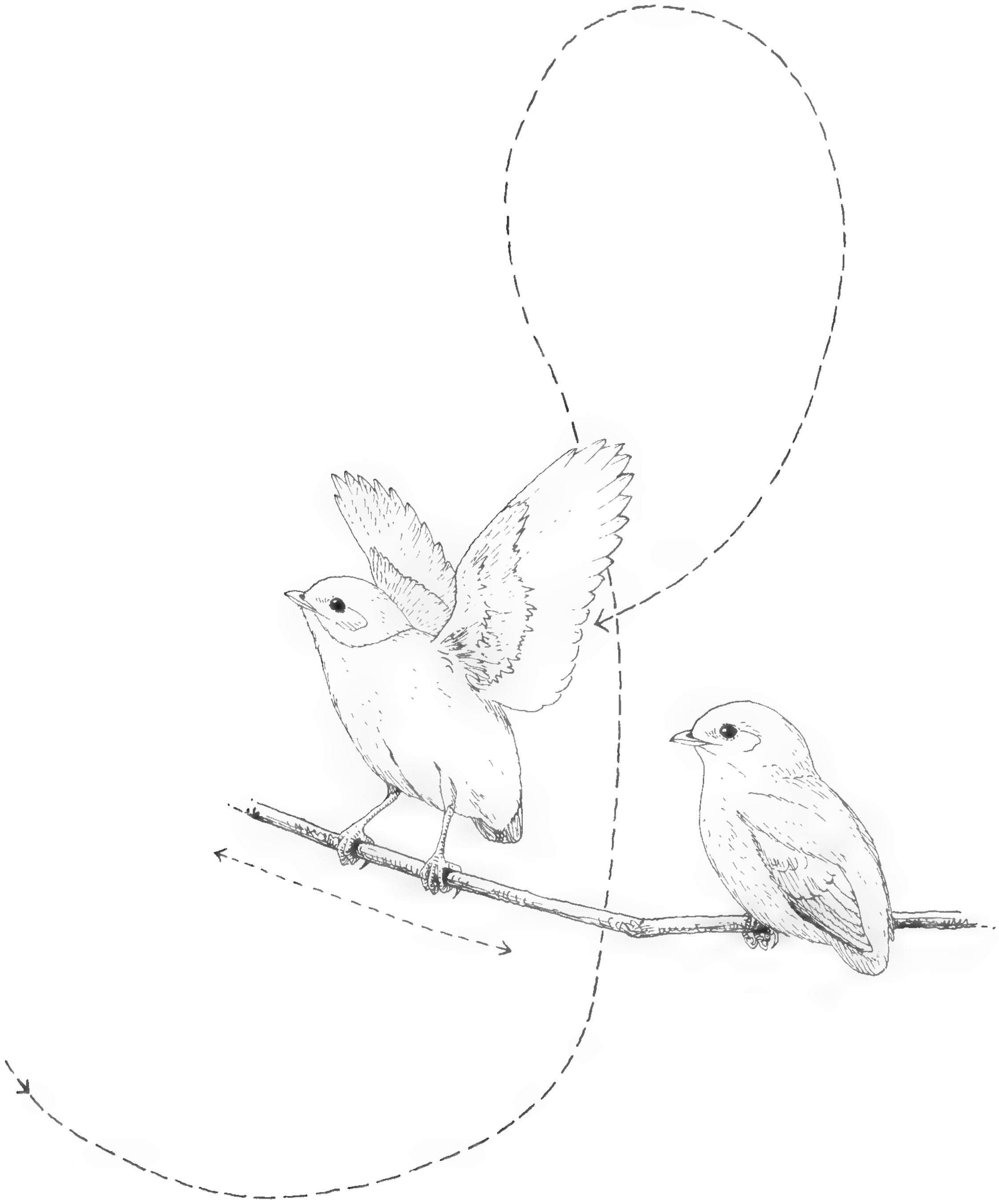

Figure 2. Courtship display of *Pipra erythrocephala*. An adult male lands beside a female after his display flight. Just before landing the male describes an S-curve in front of the female.

raised (Figure 2). Then he repeats the display flight, accompanying it with a strong, dramatically enforced vocalization during the return, and ends the call with two to three shrill *gäh* sounds delivered on landing. Occasionally, the male performs the display flight in silence. If no female is available, the male displays alone or attracts another male. Under these conditions, the performances are the same, except that the main display flight is generally substituted by curious jumps on the branch (Sick, 1959a).

The differences between *P. e. rubrocapilla* and nominate *P. e. erythrocephala* seem to be not as large as pointed out by Snow (1962b) in his excellent paper on this species. For example, the *tsack* during wing-flicking in *rubrocapilla* is vocal, not instrumental, although it resembles to some degree the mechanical snaps of other manakins. A real difference is that *erythrocephala* often makes a sharp *buzz* as it lands after a display flight, a sound probably produced by its very short, stiffened tail. *Rubrocapilla*, on the other hand, with its longer and weaker tail, only renders a vocalization, but one that resembles the mechanical *buzz* of the nominate *erythrocephala*. Morphologically, *erythrocephala* and *rubrocapilla* might be different species (de Schauensee, 1966).

Another species with only scarcely modified flight feathers is the Band-tailed Manakin, *P. fasciicauda* (see Plate 1). The yellow male, washed with crimson and wearing a black mantle, makes a hard *brrrr* as it approaches the display twig with a rapid upsweep. The sound is probably produced by the short, somewhat stiffened tail. During perching, the *brrrr* is followed by a hollow *dlock* or gong sound. The bird stamps hard on the twig and violently closes his wings. As pointed out elsewhere (Sick, 1967, in press), there are good reasons for lumping *P. fasciicauda* with *P. aureola*, when one considers not only their morphology, as have other authors, but also the similarity of their calls. Their courtship behavior must be studied more carefully. Snow (1963a) first reported on the display of the Crimson-hooded Manakin (*P. aureola,* also called the Orange-headed Manakin). The most striking display of this form is a coordinated performance between two males in which one flies with a special display flight toward the other. Snow mentions two mechanical noises made during the display.

The Red-capped Manakin (*Pipra mentalis*) makes a "surprising loud noise" as he approaches his perch after a display flight (Skutch, 1949). The somewhat stiffened tail of this small, black manakin with red head and yellow thighs probably produces the sound. The most remarkable aspect of the Red-capped Manakin's external morphology is the enlarged, curved, and stiffened secondaries. Rapidly raising his wings, the bird produces a single sharp *snap* each time he leaves the perch; more rarely, the bird gives a snapping roll. Both sounds are similar to the corresponding, but louder, noises made by *Manacus.*

Corapipo

Formerly, the Amazonian *Corapipo* was included with *Pipra*. The representatives of *Corapipo* are black with dazzling white throats. After chasing the female with whirring flight (lanceolate first primaries), the male crouches with bill pointed upward displaying the white throat. Before copulating, the male displays with a slow undulating crawl on a log, with wings fully spread horizontally, revealing white wing-bars (Davis, 1949, on the White-throated Manakin *C. gutturalis*). The White-ruffed Manakin (*C. leucorrhoa*), possibly conspecific with *gutturalis,* reportedly performs a slow display flight with rapidly vibrating wings that cause a humming sound. At intervals the male makes explosive *puff* sounds (Aldrich and Bole, 1937) that may be attributed to violent wing-beats.

Ilicura

Another quite isolated manakin is the monotypic Pin-tailed Manakin (*Ilicura militaris*) from southeastern Brazil. Its most prominant feature is a pair of elongated central rectrices that turn up at the tip—not down as in *Chiroxiphia*. It has black above, white below with scarlet plumes and rump. In display it uses the horizontal part of a large branch (see *Corapipo*) uninterrupted by leaves, epiphytes, and small twigs. It lands on one end of the display branch in a flat, crouching attitude so that its breast touches the wood; the tail points up. It faces ahead and remains absolutely motionless for a minute or so. Then the male darts obliquely upwards toward the other end of the runway. At the highest spot of the trajectory, about 30 cm above the branch, he makes a loop, producing an incredibly loud and harsh *prrrrk*. Upon landing the

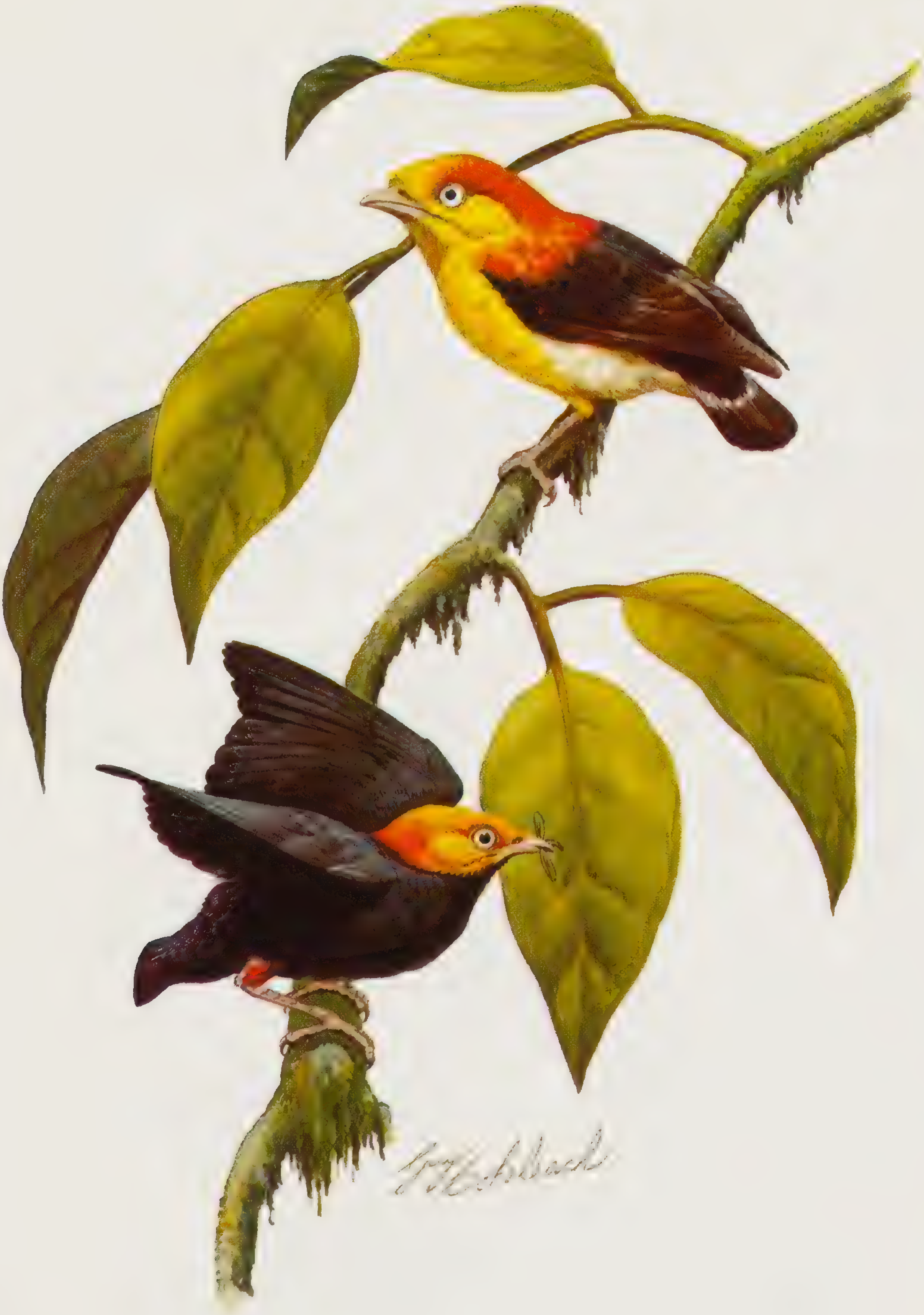

Plate I. Above, the Band-tailed Manakin (*Pipra fasciicauda*); below, the Golden-headed Manakin (*Pipra erythrocephala*). Painting by Guy Cohleach.

male turns about immediately to face his flight direction (Figure 3). The instruments that make the mechanical *prrrrk* sound must be the first primaries which are stiffened and curved in a special manner. Young males are also able to produce the same, although weaker, noise. In normal flight the males make a loud rattling noise with their wings; but they can also fly silently.

Machaeropterus

The displays of both the Striped Manakin (*M. regulus*) and the Fiery-capped Manakin (*M. pyrocephalus*) manifest one of the peaks of development in the courting behavior of the Pipridae. Two males perch together, one clinging to a slender vertical twig in a head-downward position (Figure 4). The hanging male then begins to whirr *zssssss*, grasshopper-like, and turns so rapidly back and forth on the perch that he becomes blurred to the observer. The wings are not raised; the tail is sometimes spread and shivering (Sick, 1959a). The secondaries that probably produce the sound are club-shaped and enlarged, forming small sounding boards which may greatly favor the resonance of the quills; the tail is also stiffened. The male apparently remains silent vocally during the display, although the bill is wide open—contrary to *Chiroxiphia*. For visual effect the bird exhibits his large bright crown. The Fiery-capped Manakin also shows a series of conspicuous black eye-spots on the upperside of the closed wing. The inside of the mouth does not appear conspicuously colored. When in normal level flight or when preening and shaking the body, the Fiery-capped Manakin renders a very strong clinking noise, apparently produced by the secondaries.

Allocotopterus

The morphologically similar Club-winged Manakin (*Allocotopterus deliciosus*) has still more elaborately developed secondaries — one of the strangest transformations in feather structure known among birds. The ulna is considerably thickened (Kleinschmidt, 1935:220). When displaying, the male remains alone on a horizontal twig and flashes the wings upward producing two clicking sounds—*tip, tip*. After a pause the wings are held up again and rotated downward with a buzzing *wherrrr* (Willis, 1966). The *tip*

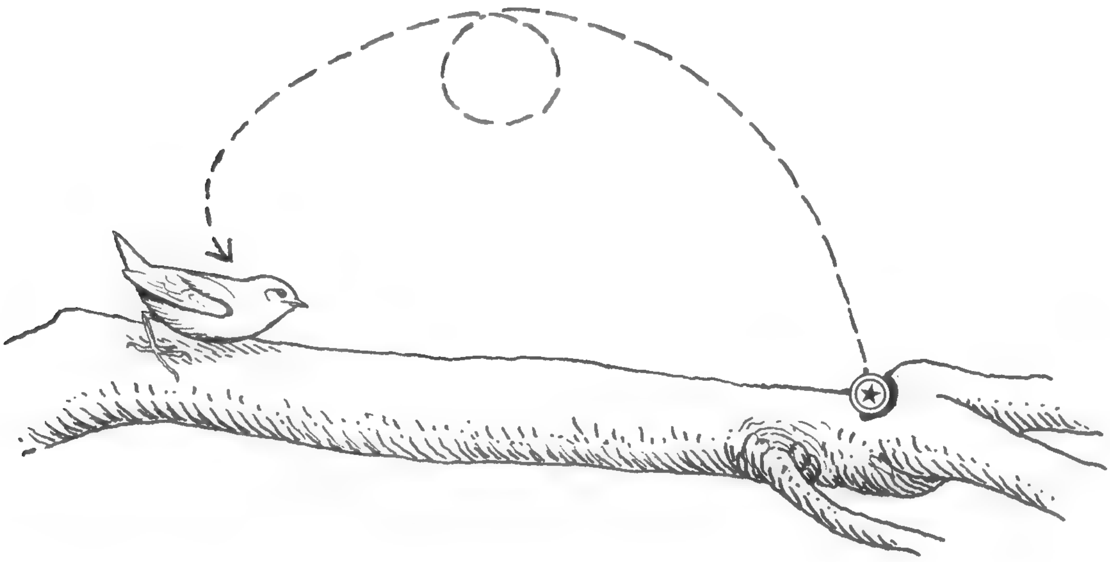

Figure 3. Courtship display of the Pin-tailed Manakin, *Ilicura militaris*. A single male displays alone on a large branch, making a complete loop accompanied by a loud, harsh *prrrk*. In a crouching attitude, the male's breast seems to touch the branch.

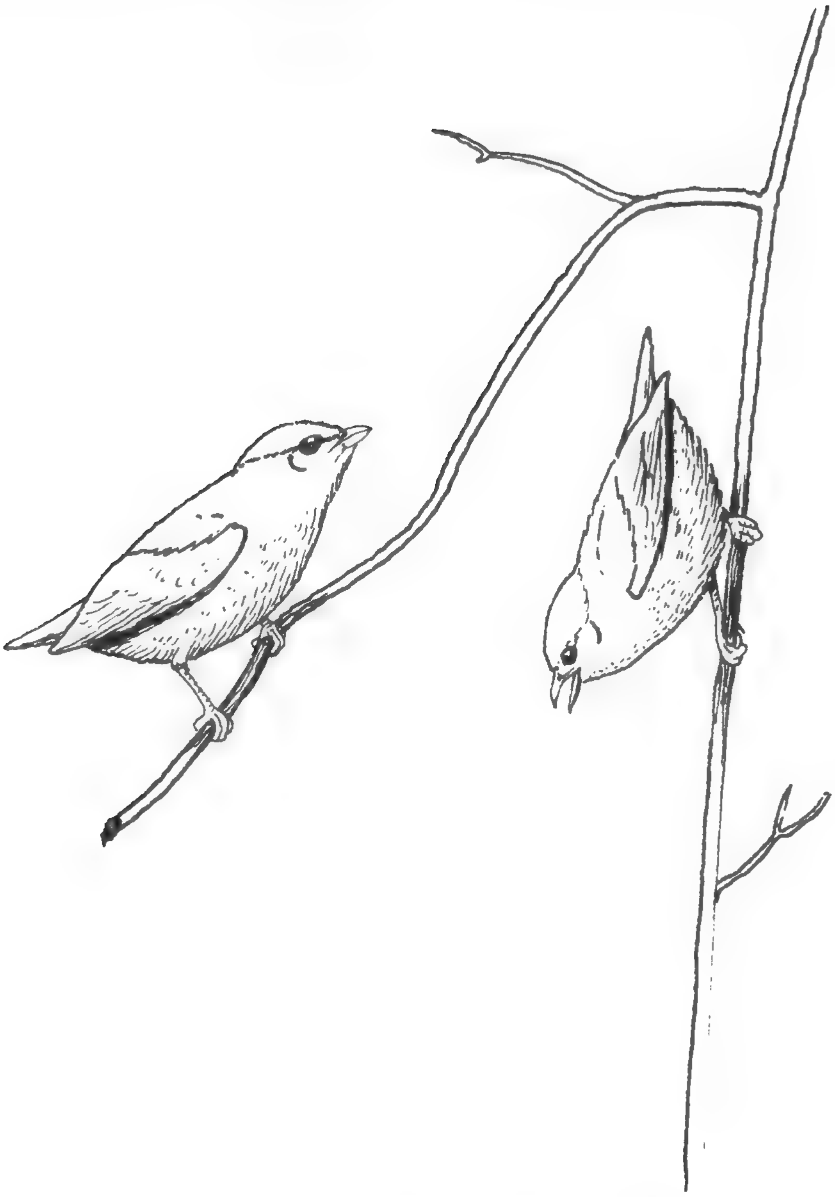

Figure 4. Courtship display of the Fiery-capped Manakin, *Machaeropterus pyrocephalus*. Two males perform in the same tree but on different twigs.

(not produced by *Machaeropterus*) must correspond with the feather beating in *Pipra mentalis* and *Manacus,* the *wherrrr* probably with the grasshopper-like *zssssss* of *Machaeropterus.* Raising the wing and showing the tail from below resembles displays of *Pipra.* While the display of *Machaeropterus* emphasizes dorsal visual effect, the performance of *Allocotopterus* appears to be more conspicuous from the rear. In normal flight, *Allocotopterus* reportedly remains silent. The literature does not mention calls of this manakin.

The acoustic effects of the display in *Machaeropterus* and *Allocotopterus,* as far as known, are not so surprising when one considers the fantastic equipment these birds possess for the mechanical production of sound. Most impressive is the clinking noise produced by the Fiery-capped Manakin during normal flight.

Manacus

I have referred repeatedly to the outstanding antics of the White-bearded Manakin (*Manacus manacus*). When the displaying male enters the cleared court near the ground and jumps in a fixed pattern (left turn or right turn) back and forth between two to four upright saplings, he makes a very sharp *crack* with each jump. He always lands facing toward the sapling from which

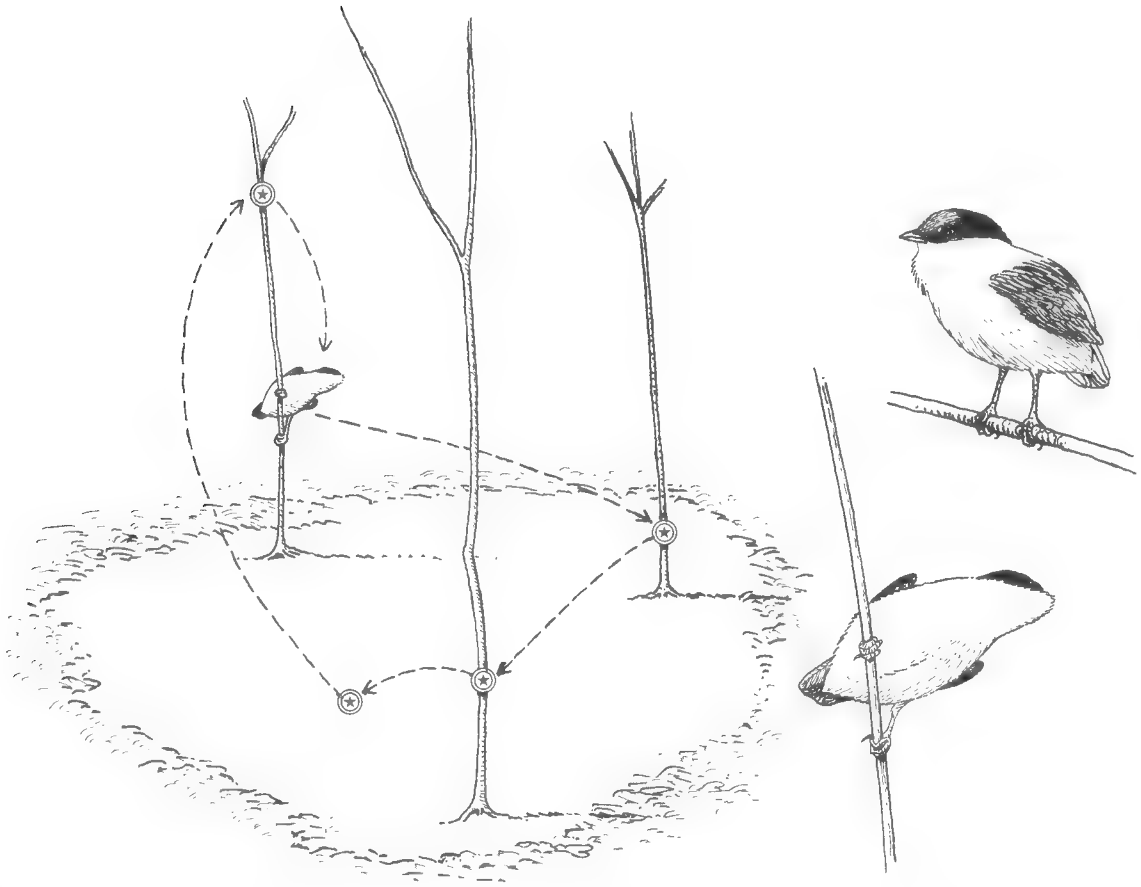

Figure 5. Snapping display of the White-bearded Manakin, *Manacus manacus*. The male is performing alone. Station 4 (*lower left*) is situated on the ground which the male has more or less cleared of leaves and sticks. Two enlargements show a male (*top*) about to perform and another (*bottom*) at the beginning of a snapping display.

he came. The male assumes a horizontal position across the sapling, with the head thrust forward and the beard fully extended (Figure 5). Finally, he jumps on the ground and then back higher up into the sapling, producing a loud grunt. The jumps to and from the ground are so powerful that fallen debris on the court is blasted away, resulting in a cleaner court. The bird renders no vocalization during the entire display; nor does one hear the whirring sound produced during flight by the primaries. The male of this manakin does not fly during solo display—he only jumps.

The *crack*, sometimes rapidly repeated to produce a roll, is apparently the result of highly modified secondaries: thickened shafts, stiffened outer webs, quills not attached to the ulna but with strong muscle slips attached to their base, and a flattened radius (Lowe, 1942). With raised wings the secondaries are beaten together. Immature, green-plumaged males give a weaker *snap* and *grunt*. On 13 November 1939, I collected a young male which had developed the *crack* and noted that its secondaries were only slightly curved and stiffened—in fact, less so than in an adult female with which it was compared. I therefore assumed that the snapping sound did not originate from the secondaries (Sick, 1959a). The young, green-colored males cannot produce the flight whirring of the wings which is a typical sound of adult males not engaged in display.

For females which come to the court, males have an additional display that includes "fanning" and a "slide-down-the-pole" (Snow, 1962a).

The highly ritualized solo display of the White-bearded Manakin at its court on the ground derives and often receives its stimulus from a completely confused group display that sometimes precedes the solitary performance. Three or more males (both adult black-and-white and immature green males)

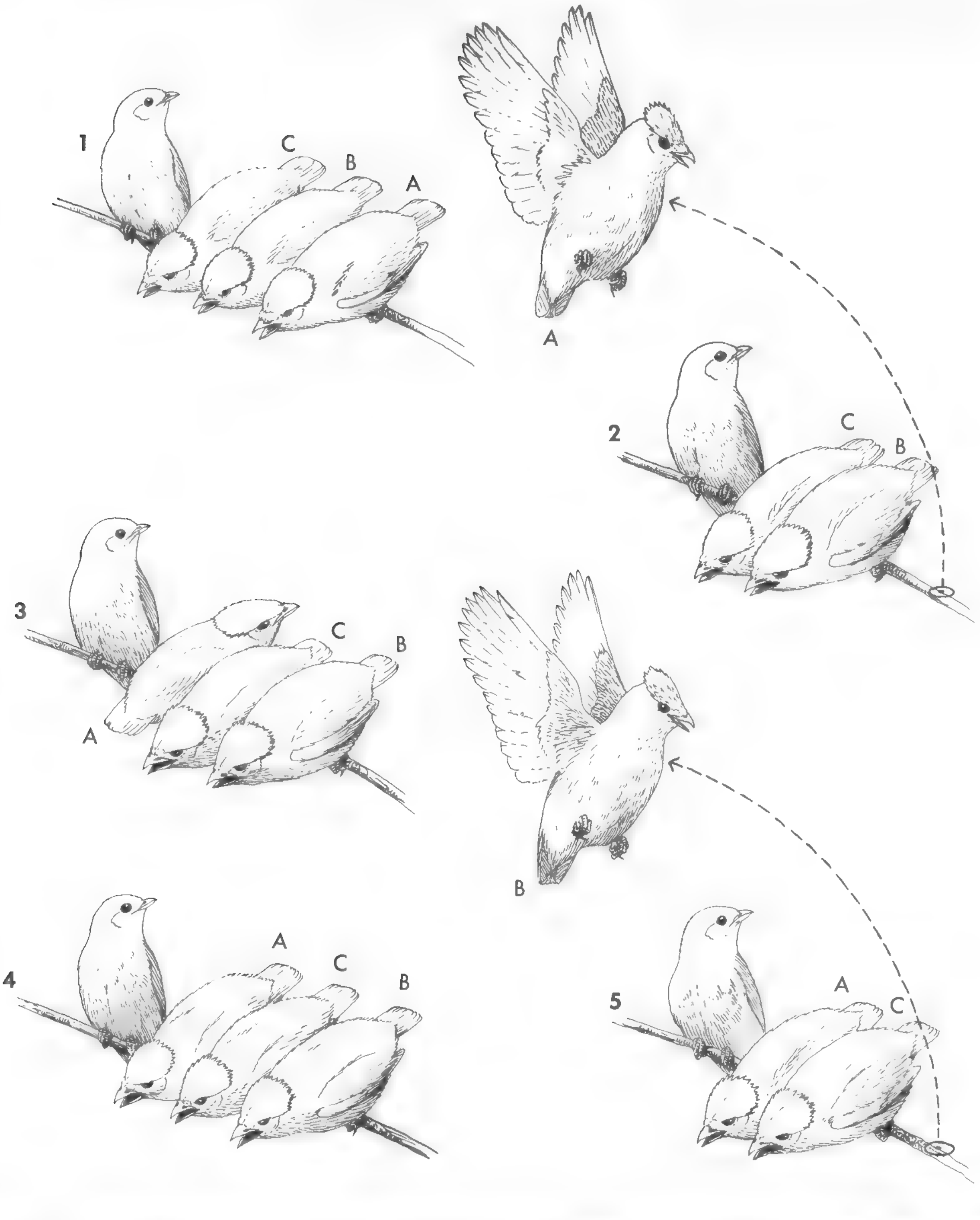

Figure 6. Courtship display of the Swallow-tailed Manakin, *Chiroxiphia caudata*. Three males are performing before a watching female.

perform together higher up on different branches, using all the sources of sound production, both vocal and mechanical, ever acquired by this manakin. What a contrast between the solo and group displays: In the former, the only sound is the loud instrumental *crack* as the male jumps swiftly from sapling to sapling. In the group display, the sound becomes a wholly unrhythmical and uncoordinated muddle as several males concomitantly use all the sounds, including all vocal ones, available to their species.

Instrumental, or mechanical, sounds in *Manacus* represent a higher degree of evolution than vocalization. The solo display probably provides greater stimulation for the female acoustically than visually, since the movements are too rapid to show colors (black and white).

Males commonly maintain several to many courts in a limited area. They use them simultaneously during periods of intense display, each owner on its respective court. Several males may display on the same court, but not at the same time. The term "lek" has been applied to manakin displays in which several males perform in concert on their nearby courts. Leks originally described the assemblies of courting Black Grouse (*Lyrurus tetrix*) in northern Europe. The term "arena" has also been applied to courting grounds in manakins. Lek behavior evolved convergently in diverse birds: some gallinaceous birds, the Ruff (*Philomachus pugnax*), hummingbirds, and some passerines including birds-of-paradise (Paradisaeidae), bowerbirds (Ptilonorhynchidae), weaverbirds (Ploceidae), cotingas (Cotingidae), and of course manakins (Pipridae). Among the Pipridae only *Chiroxiphia* manifests a truly communal display; the group displays of *Manacus* are undertaken by rival males that show no coordination of their court activities.

Chiroxiphia

An amazing communal behavior evolved in the Swallow-tailed Manakin (*Chiroxiphia caudata*). Two to three males and one female gather to display. The males (blue with red crown, black wings and tail) perch closely side by side, in a row, on a slightly sloping (or horizontal) twig, face the same direction, all crouched, tripping, forming a vibrating mass (Figure 6). They call in the recurrent rhythm of a perfectly synchronized "frog chorus." Suddenly the lowest male on the twig rises straight into the air one to two feet and hangs momentarily suspended facing the female. He delivers a sharp *dik-dik-dik,* then lands at the upper end of the row of males at the side of the motionless female. He pivots immediately in the direction of the other males and joins the other males in tripping. Now the lowest bird performs in a similar manner, and so on. The entire performance occurs rapidly, giving the impression of a turning wheel; the speed varies.

The males will perform in the absence of a female, showing preference to a green-plumaged male as the substitute for a quietly perched female. In this case uncoordinated jumps are often substituted for the hovering display-flight. The plumage of a first-year male is entirely green, like that of the female. In the second year the subadult male has green with a red crown. The fully adult plumage of the male, according to observations made in captivity, is not acquired until about three years.

The performing males manifest no agonistic behavior toward one another, quite in contrast to *Pipra* and *Manacus*. Copulation is preceded by a different display between a single male and a female, as described for the Long-tailed Manakin, *Chiroxiphia linearis* (see Frontispiece), by Wagner (1945) and for the Blue-backed Manakin (*C. pareola*) by Snow (1963c).

The most astonishing aspect in the communal display of *Chiroxiphia* is the perfect coordination of the entire performance, both in movements and calls. And still more unusual is that, in the absence of a female, not all participating males play an equal part. The male, generally a female-colored green one, which plays the female role behaves in a basically different manner from the other interacting males. He is clearly subordinated since the flock establishes a hierarchy of social dominance. Only when no more than two males are present during the display do they behave equally, both tripping and jumping.

The antics of the other species of *Chiroxiphia* are all basically similar to one another, especially in the "cartwheel dance" (courtship display described for *C. pareola* by Gilliard, 1959; Sick, 1959a; Snow, 1963c; and for *C. lanceolata/linearis* by Friedmann and Smith, 1955; Slud, 1957; Wagner, 1945). In spite of this likeness, much remains to be studied and analyzed, as pointed out by Slud (1957:3). Some authors, for example, mention snapping sounds for *C. linearis,* which others, including myself, have never heard for *C. caudata* and

C. pareola. Certainly *C. caudata,* at least, is unable to produce mechanical noises other than wing rattling; the main display, however, does not include a wing rattle.

Display of Young Males

Young, female-colored males of conspicuously clad species generally behave like fully adult males. Observers who failed to collect or band such birds could not confirm the sex of the green manakins interacting with others during courtship. Nor could they solve the complexities of the displays involved. Green-plumaged birds of *Pipra erythrocephala* and *Manacus manacus,* which performed the complete display of their species, showed, when collected, testes as large as adult-plumaged males. On the other hand, the testicular development in green males of *Chiroxiphia caudata* was not always equivalent to that of the adult males. These immature males often substitute for the passive female during the communal display of fully adult males (Sick, 1959a). Green males of *Chiroxiphia* can perform among themselves. Green males of *Manacus* sometimes display between courts. Occasionally, rudimentary performances occur among other young manakins as well as in fully adult-plumaged birds.

The Female on the Court

There is no pair bond in typical manakins. The female's social contact with the male usually occurs only on the display ground. There she arrives quietly and secretively. Only exceptionally does the female utter the advertising call of the male, and when she does it is more subdued (specimen of *P. erythrocephala* collected). The female either passively watches the proceedings on the court, or she may even participate mildly in the courtship (*P. e. rubrocapilla*). For *Manacus,* Snow (1962a) reports a highly coordinated dance between a male and female; moreover, he found that the females, which were banded, went from one male to another.

If two females meet on the display perch, the more active one drives away the other (*P. e. rubrocapilla*). The arrival of a female immediately stimulates the performing male. When a female approaches the vicinity of the arena, the male flies to the court to dance. Only later does he try to copulate (*P. erythrocephala, M. manacus*). In some species special displays precede copulation. The male mounts either directly as he returns from the display flight (*P. e. rubrocapilla*) or a short time after landing by the side of the female (*P. e. erythrocephala*). Copulation can take place with little prior courtship and sometimes distant from the court. If the female deserts the court, the male displays less intensely or ceases (*P. erythrocephala*).

Certain males are outstandingly successful in attracting females. Snow (1962a) reported that 20 color-banded females, plus a number of unbanded ones, visited a single male on his court, which shows the extremely polygamous nature of these birds. Males manifest a strong sexual activity on their courts. One male Golden-collared Manakin, when confronted with a stuffed female placed on its court, mounted, or tried to mount, the dummy 163 times in three hours (Chapman, 1935). Such conditions are, of course, completely unnatural. Normally, copulation is seldom seen. Gilliard (1959) never succeeded in seeing a copulation on the "bowers" of *Chiroxiphia pareola.* Mating in *Chiroxiphia* usually takes place some distance from the main display perch.

Functions of Courtship Displays

The courtship performances of manakins obviously attract and stimulate the females. Gilliard (1959) proposed another function of the group dances in manakins: that social dancing between the males replaces fighting in the selection of the dominant breeding stock. In the Cock-of-the-Rock (*R. rupicola*), Gilliard (1962) concluded: "Arena behavior is courtship behavior as reshaped by emancipated males to include their non-discardable nesting tendencies." Wagner (1962) questioned that the performances of manakins serve to attract females. His assumption that the dances between some interacting males are mere idle work ("Leerlauf") does not invalidate the conclusion that the displays are originally directed to the female and that they are, indeed, "love antics" as suggested by Darwin (1871).

As mentioned previously, in the communal display of Swallow-tailed Manakins a female-colored male often plays the stand-in role for an absent female. In this genus (*Chiroxiphia*) attempted copulations between males do occur. In *Pipra* and *Manacus* the males often show considerable aggressiveness toward each other on the courts, even rolling together on the ground.

It is quite obvious that sexual selection in manakins is the female's choice. During evolution, sexual selection favored an increase in sexual dimorphism toward the development of exaggerated signal characters of all kinds, as shown among male manakins. In the female, on the other hand, natural selection favored the retention of cryptic plumage that better conceals her as she assumes the sole responsibilities of nest-building, incubation, and parental care. As pointed out by Gilliard (1962), the biological advantage of this form of breeding behavior is probably that a smaller percentage of each generation of males is needed for the perpetuation of the species, permitting more severe selection and consequently more rapid evolution.

Interspecific Interaction

The vigorous display in a group of *Manacus* courts occasionally seems to induce the neighboring Golden-headed Manakins and Striped Manakins to go to their own display branches and perform. No one has yet reported a manakin appearing at the court of a different species. Since the females of many manakins are generally drab and uniformly colored, and since courtship and copulation are largely restricted to the courts, hybridization could probably result if a female chances upon a male of another species performing on his court. Frequent hybridization occurs in birds-of-paradise and hummingbirds, both of which maintain courts or arenas. In manakins, however, hybrids are rare (Parkes, 1961). Snow (*in* Parkes, 1961) reports a juvenile male *M. manacus* displaying persistently to a female-plumaged *Pipra erythrocephala,* almost certainly a juvenile male. Stuffed females of other species of manakins were placed on the courts of the Golden-collared Manakin and were mounted by the owner of the court (Chapman, 1935).

The absence of closely related congeneric species in the same region acts as an obvious isolating mechanism. I, and others, have observed this distribution in Brazil and other parts of South America. In the Upper Xingú, Mato Grosso, for example, *Pipra erythrocephala* lives together with *Xenopipo, Chiroxiphia pareola, Machaeropterus pyrocephalus, Heterocercus lineatus, M. manacus, Tyranneutes stolzmanni,* and occasionally *Pipra nattereri.* In Espírito Santo, I have frequently seen *M. manacus* and *Pipra erythrocephala* drive away *Machaeropterus regulus* when they meet in the woods.

Court Displays in Cotingidae and Tyrannidae

Similar shifts of evolution occur in unrelated groups widely scattered over the world. Nevertheless, it may not be due to convergence that the elaborate courtship display of manakins has counterparts in some cotingas. The thin and vague morphological boundaries that separate these families are paralleled by behavior patterns that emphasize how closely related these two families are.

The thrush-sized Purple-throated Fruitcrow (*Querula purpurata*) is a black cotinga with a red neck-collar. It lives in the canopy of the Amazonian forests and is a typical arboreal arena bird. Its courtship, accompanied by loud and continuous calls, resembles the display of manakins in several ways: a moustache display similar to *Heterocercus;* a quivering of flight feathers that recalls *Pipra;* a melodious voice that not only links it with other cotingas but also with the manakin *Antilophia.* Similar behavior occurs in the large Red-ruffed Fruitcrow (*Pyroderus scutatus*) and in the Guianan Red-Cotinga (*Phoenicircus carnifex*). These cotingas perform in noisy groups. As far as is known, the sexes do not form pair bonds. *Schiffornis,* still considered manakins by systematists, lives solitarily and advertises with a melodious call and without special postures. Its nesting in hollow trunks, the type of nest material (leaves), and its diet of large, hairy caterpillars and fruits with big seeds strengthen the opinion that these birds are probably cotingas, not manakins.

Sometimes the famous Cock-of-the-Rock (*R. rupicola*) of northern South America is considered a large, aberrant manakin. As pointed out by Gilliard (1962), its courtship display is essentially a silent ground-visiting lek performance which is exclusively visual: a motionless, "frozen" exhibition of the brilliantly orange plumage in a crouching posture. This cotinga also displays in a very slow and deliberate manner. Preceding the main display, the males perform on branches near the arena with head-bobbing, little hops and wing-flicking, various calls, and snaps said to be made with the bill—acoustically very similar to the snaps emitted by *Manacus.* The display of the Cock-of-the-Rock thus reveals some components which, indeed, link it to the Pipridae. On the other hand, there are strong differences, such as the lack of motion and sound during the main display. That *Rupicola* may be more closely allied to the cotingas is suggested, too, by the structure of its nest (heavy mud nest on walls). The females live apart from the polygamous males and breed colonially. Gilliard (1962) believes that the species most similar to *Rupicola* in its arena behavior is Jackson's Widow-bird (*Drepanoplectes jacksoni*), an African grassland passerine.

Some tyrant flycatchers (Tyrannidae) also show somewhat manakin-like behavior. The dull-colored *Pipromorpha* are solitary birds that advertise tirelessly, singing and flipping their wings (Skutch, 1960). In emancipation from nest duties it equals *Myiobius,* other small tyrant flycatchers that share the shadowy woodlands with *Pipromorpha. Myiobius* hop and flit about the whole day, displaying bright yellow rumps with tails spread and wings drooped. These movements have nothing to do with courtship, but are due to a general agitation in these excitable birds. Occasionally, I have observed somewhat similar behavior (crouching, pivoting, and spreading of wings and tail of solitary birds) in the Tropical Pewee (*Contopus cinereus*), a small olive-gray flycatcher known to be monogamous (Skutch, 1960). In the Planalto Tyrannulet (*Phyllomyias fasciatus*), on the other hand, three or more birds, including females, gather and chase one another and call constantly. This behavior resembles that of the Black Manakin. Both species have a plumage that lacks striking signals.

When we look for comparable courtship behavior in the closely related cotingas and tyrant flycatchers, and find similarities, we can understand some of the steps reached in the evolution of displays that led to what we regard today as typical performances of manakins.

Summary

Proceeding from general statements on morphology and speciation, I have presented a comparative review of the various types of courtship behavior in manakins, treating more than 20 species, mostly observed by me. Special attention is given to the source of sounds, particularly mechanical sounds generally produced by modified flight feathers. The peaks of evolution are reached in the acoustically unique solo display of *Manacus,* the outstanding instrumental equipment of *Machaeropterus,* and the fully synchronized performances of *Chiroxiphia.* Reports on the behavior of females, young males, and interspecific interactions lead to a better understanding of function of manakin displays. Similar displays in cotingas and tyrant flycatchers are of phylogenetic interest.

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OBSERVATIONS ON GALÁPAGOS TOOL-USING FINCHES IN CAPTIVITY

GEORGE C. MILLIKAN AND ROBERT I. BOWMAN

Among the puzzling finches endemic to the Galápagos Islands are those which use cactus spines or twigs as an extension of the beak to extract insects from narrow cracks and crevices. In the "Woodpecker Finch" (*Cactospiza pallida*), the subject of our study, this behavior—described as "tool-use" or "tool-using"—has attracted the attention of several scientists: Gifford (1919), Lack (1945, 1947), Bowman (1961), Eibl-Eibesfeldt (1961), and Eibl-Eibesfeldt and Sielmann (1962). In the Mangrove Finch (*Cactospiza heliobates*), a close relative, Curio and Kramer (1964) have recently noted a similar behavior.

We may draw an analogy between the twig used by *C. pallida* and a human tool, because both objects in some way alter the position or form of a second object. For instance, a hammer in the hand of a human can change the position of a nail in a block of wood, and similarly a twig in the beak of *pallida* can change the position and sometimes the shape of the food which is removed from a crack.

When this relationship between an active and a passive object is considered, we find that only a few birds besides *pallida* characteristically use tools. The Northern Shrike (*Lanius excubitor*) often stores food—insects, small rodents, and birds—by impaling them on a fixed spine (Forbush, 1929), or in the forks of branchlets in trees and shrubs (see the paper by Tom J. Cade in this issue of *The Living Bird*); and several other birds may use spines or forked sticks to anchor a carcass while they flay it with the bill. This is an example of a fixed device which serves as an extension of the body—in this case, talons—and is used to alter other objects (i.e., to process prey). Another example of tool-using is the habit learned by several captive and wild birds of pulling up a string to which food has been attached (Thorpe, 1956). Since birds swallow the food but not the string, they apparently distinguish between the two objects.

The Satin Bowerbird (*Ptilonorhynchus violaceus*) of Australia holds a wad of fibrous bark in its mouth when it smears berry juices on the wall of its bower with the side of its beak (Marshall, 1954). The bark has frequently been cited as an example of a tool, but it is now thought that it functions as a cork, or stopper, to prevent the juices from oozing from the tip of the mandibles, and thus its action on the bower is not direct. The Egyptian Vulture (*Neophron percnopterus*) throws stones from a standing position at ostrich eggs to break them (van Lawick-Goodall, 1966), and the Black-breasted Buzzard

(*Hamirostra melanosternon*) of Australia is said to drop stones from the air onto emu eggs (Chisholm, 1954). In these cases the stone acts directly, like the twig of *pallida*, but it acts more abruptly than the other objects which we have considered as tools. The Tailorbird (*Orthotomus sutorius*) of southeast Asia stitches leaves together with plant fibers to form a receptacle for its nest (Wood, 1936), but neither the fibers nor the leaves fit our definition of a tool. This example demonstrates that tool-using is not the only kind of activity in birds which establishes complex relationships between objects.

Tool-use, some variable and some stereotyped, occurs in other groups of animals. The southern sea otter (*Enhydra lutris*) occasionally breaks the hard shell of the abalone, its chief food, by pounding it against a stone—a form of anvil—that it places on its chest, or it may strike two abalones against each other (Fisher, 1939). Wild chimpanzees (*Pan satyrus*) draw termites out of their nests in a variety of ways (Goodall, 1964). In contrast to the variable behavior of the otter and the chimpanzee, we find the highly stereotyped almost mechanical behavior of the tropical ant, *Oecophylla longinoda* (Chauvin, 1952). These ants fasten leaves together with silken threads, produced by pupae that the workers hold in their jaws and use as tools. The occurrence of tool-using behaviors in a few animals in phylogenetically distinct groups suggests that no single pattern of nervous organization produces them all, but that each has developed separately.

In studying *Cactospiza pallida*, we have considered the nervous organization from three points of view: (1) complexity, (2) controlling stimuli, and (3) evolutionary basis. We have tried to assess complexity by varying the form of tools and foraging sites and observing which behavior is stereotyped, or unchangeable, and which is variable. We have judged control (i.e., motivation) by analyzing the role of food in evoking tool-using. And we have considered the evolutionary basis of tool-using by *pallida* in relation to the manipulative ability found in related and unrelated passerine birds.

The subjects of our study were six *pallida*, five males and one female, which had been captured as juveniles on Indefatigable Island in the Galápagos archipelago. We kept them in a large communal cage provided with twigs and crevices for one year before beginning our observations, which we carried out intermittently for two and one-half years. We kept one bird in isolation for the first three months after its capture, but made no systematic attempts to restrict the experience of the other birds. We used additional passerine birds, kept in captivity for varying periods of time, for our comparative observations on manipulative ability.

Stereotypy

We analyzed the movements, by which *Cactospiza pallida* obtained food with a stick, in various situations and attempted to characterize each part of the performance as either stereotyped or variable. When we observed no alternative movements, we considered a part to be stereotyped.

Preparatory Movements.—Searching behavior seemed more prominent in *Cactospiza pallida* than in most of the other captive finches that we studied, including species of *Geospiza, Camarhynchus,* and *Platyspiza* and the far-flung Darwin's Finch, *Pinaroloxias inornata* from Cocos Island, Costa Rica. *C. pallida* frequently cocked its head at different angles and peered into cracks and nooks. It perched sideways on vertical walls and hung upside down, investigating every surface of its environment. While this finch may sometimes make use of its ears in finding insects, as suggested by Eibl-Eibesfeldt

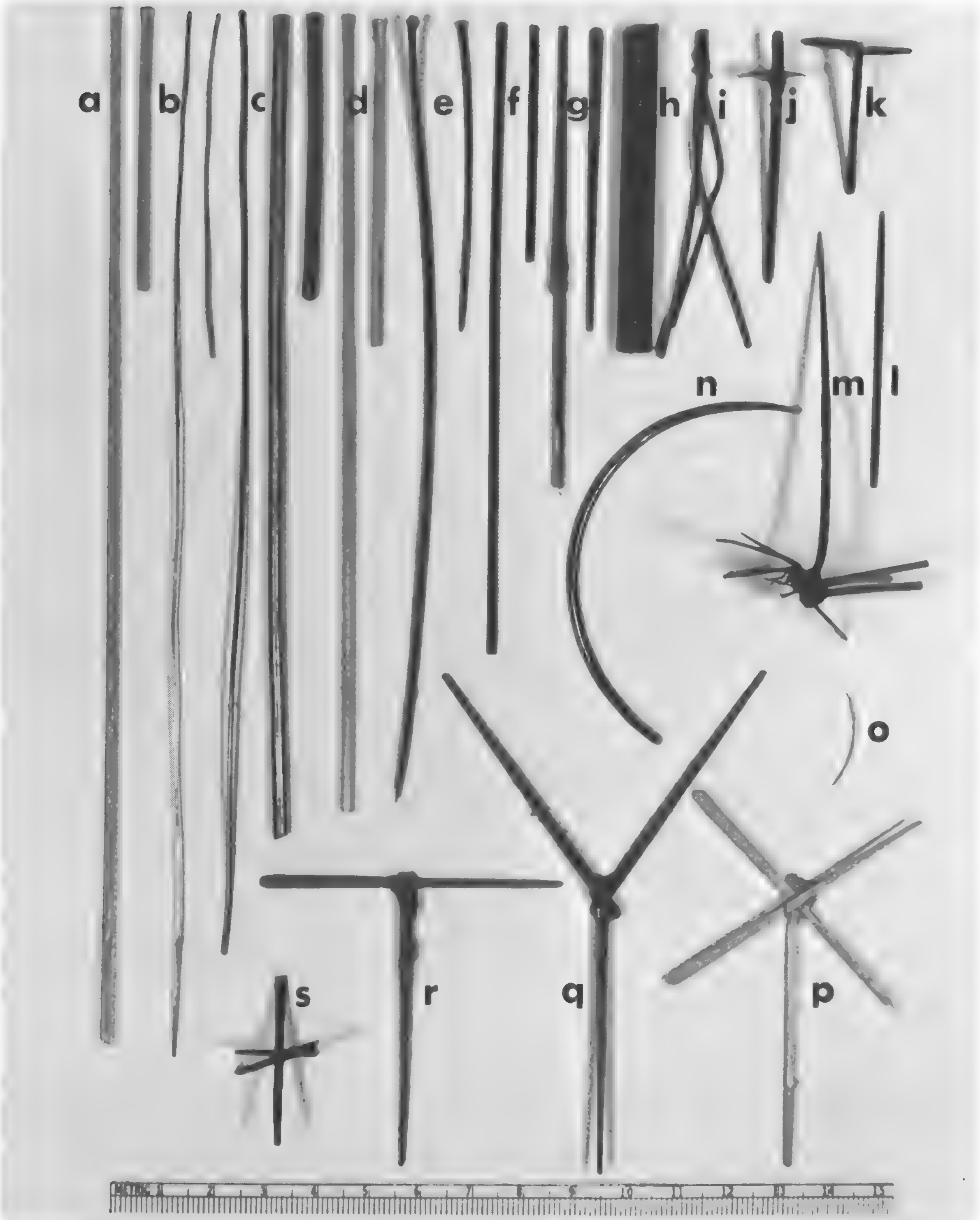

Figure 1. "Tools" made available to *Cactospiza pallida,* the Woodpecker Finch, in experiments described in the text: a, spagetti; b, flexible wires; c, metal rods; d, wooden applicator sticks; e, cactus spines; f, coping saw blades; g, toothpicks; h, wooden dowel; i, pine needle fascicle; j, toothpick with circular metal shield near one end; k, 3 toothpick pieces glued together at right angles to each other; l, metal needle; m, cactus spine cluster; n, upholstery needle; o, wood shaving; p, q, r, and s, configurations made of toothpicks glued together. Scale shown at bottom, 153 mm.

(1961), our birds easily located dead, and presumably silent, mealworms even in deep cracks. The distinctive cocking of the head while foraging probably serves more to position the eyes for seeing the holes better, than the ears for hearing the prey. The Robin (*Turdus migratorius*) displays similar head-cocking movements, but Heppner (1965) has recently disproved the suggestion that the bird is listening for its prey.

When *Cactospiza pallida* broke off a twig from a branch, either by bending or pulling, it usually held the twig at the base and only occasionally by the

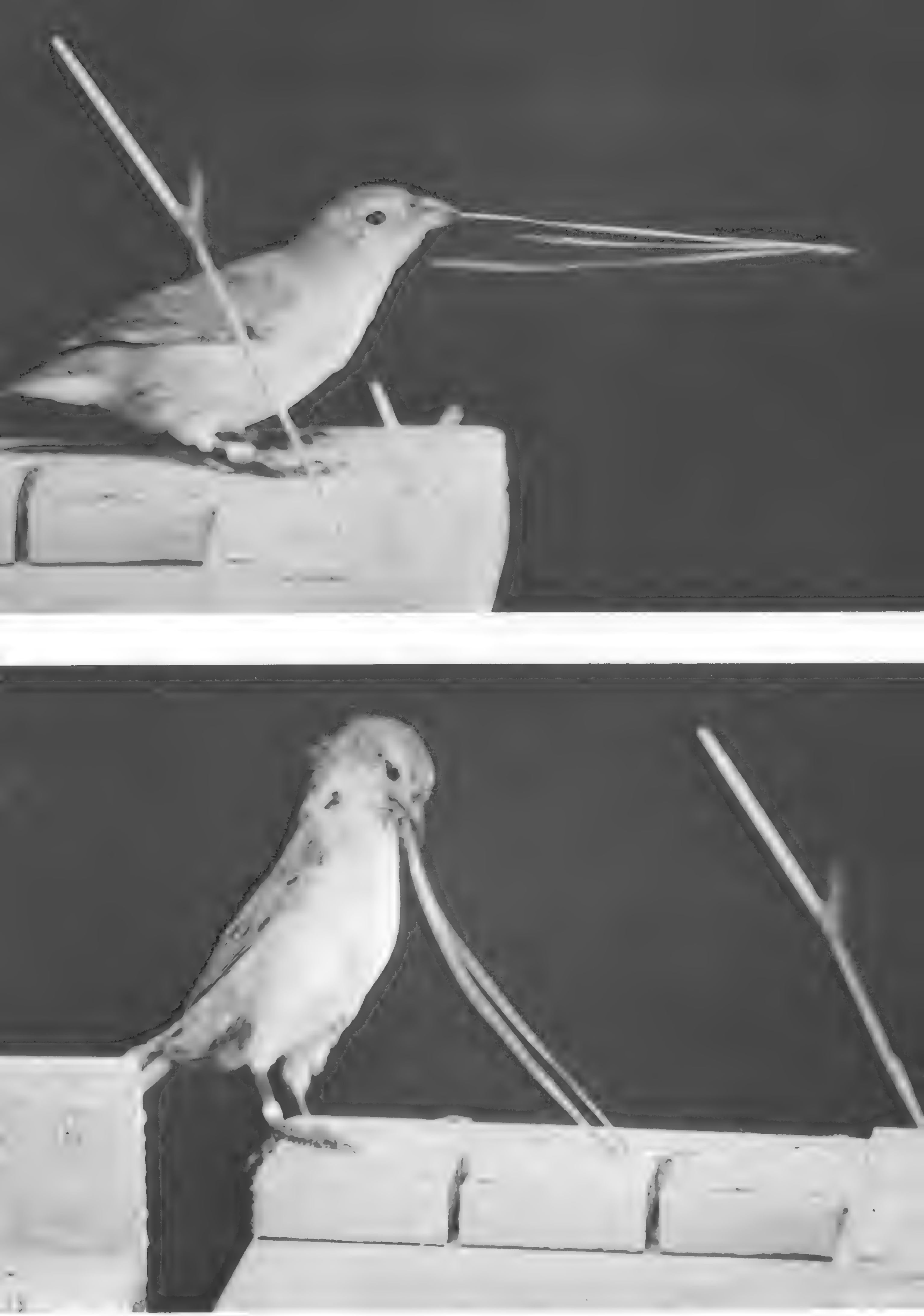

Figure 2. *Cactospiza pallida* manipulating a fascicle of pine needles. *Above:* warding off another finch approaching the food table. *Below:* attempting to insert ends of needles in a baited slot.

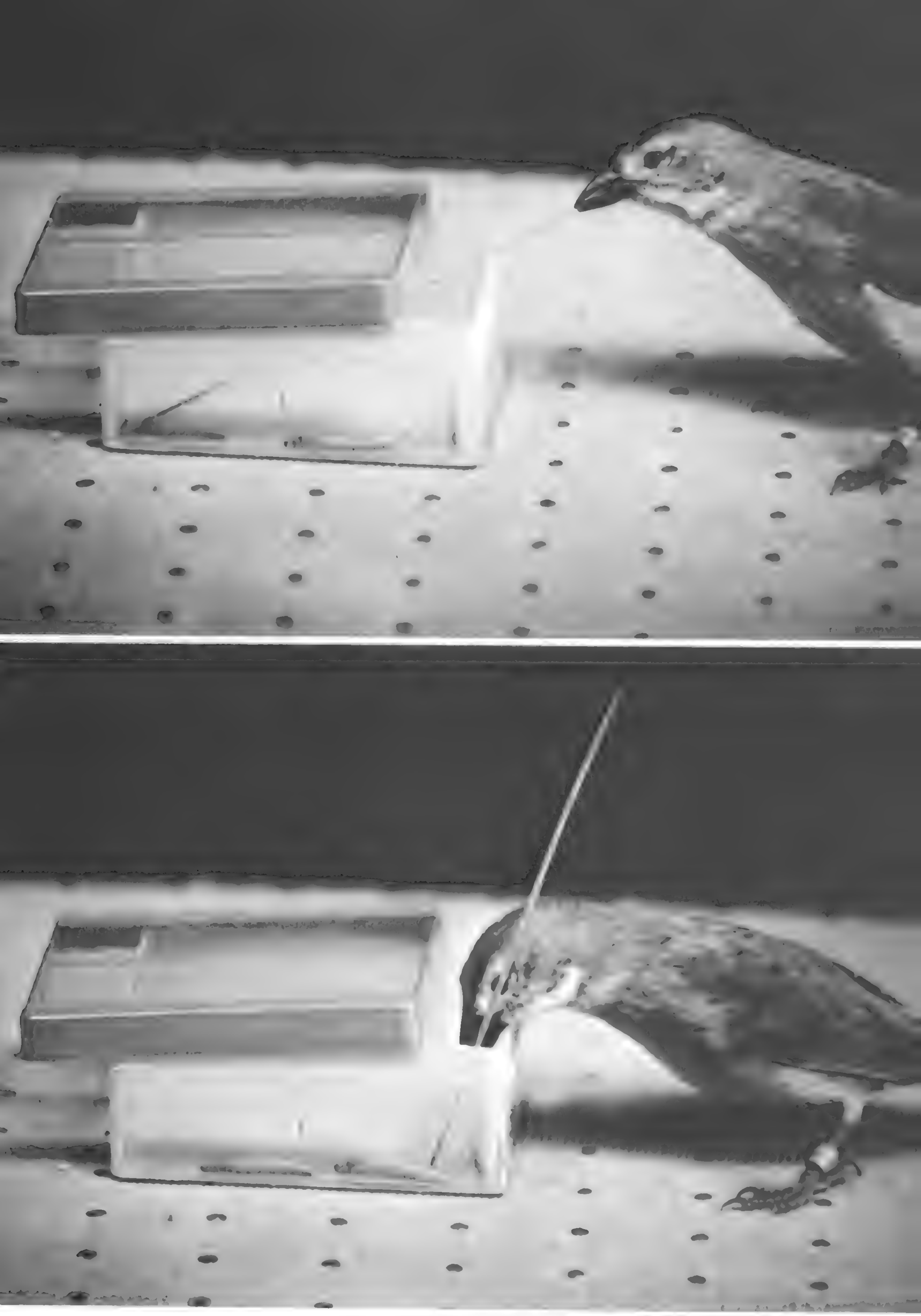

Figure 3. *Cactospiza pallida* using a six-inch cactus spine as a tool for probing at prey far out (*above*) and close in (*below*). Note how the tool is aligned with the "tomial axis of the bill" which intersects the eye posteriorly (cf. Bowman, 1961, Figure 56).

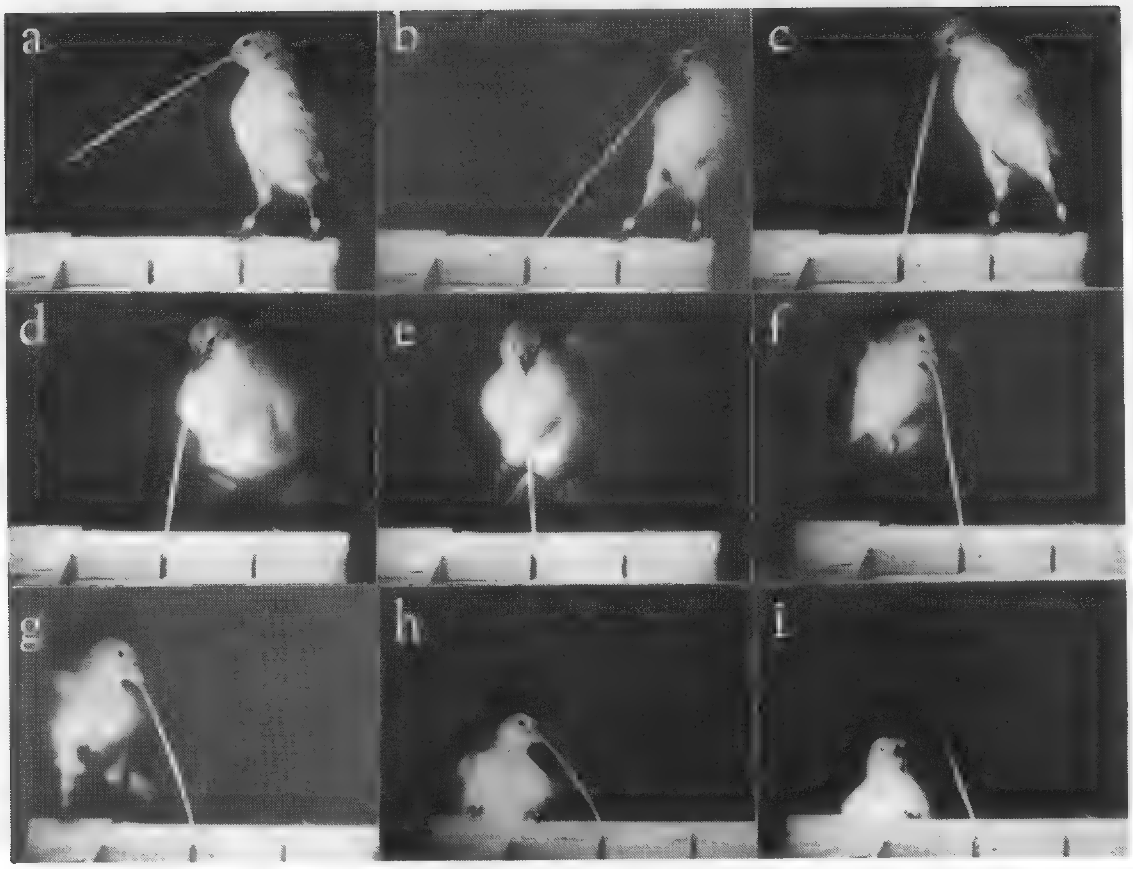

Figure 4. *Cactospiza pallida* using a tool in flight. Holding a six-inch cactus spine lengthwise in its bill (*a*), the finch leans backward with legs fully distended and head forming an acute angle with the neck (*b*). As the distal end of the cactus spine engages the crevice (*c*), the bird rocks forward and stretches its legs and neck to the utmost. Unable to insert the spine to the bottom of the crevice, the bird takes flight (*d*) in a semicircular path, pivoting on the tool (*e, f*), which has now penetrated the depths of the slot. As the bird prepares to land on the opposite side of the food table (*g*), the spine, now bending under the weight of the bird, is still firmly grasped with the bill. Finally, missing a foothold on the food table (*h*), the bird relinquishes its hold on the tool, which falls from the crevice (*i*). Enlarged from frames of 16 mm motion-picture film.

top. We judged that it preferred projecting twigs because we never saw the bird pick up a twig from the ground. Actually, Bowman (1961) reports that *pallida,* in its natural environment, rarely descends to ground level while foraging. In a few instances, it snapped a twig into two pieces after picking it up and retained the shorter piece that was a somewhat more manageable tool. When the only twigs available to the finch were toothpicks of uniform size, the bird used many as probes and broke very few.

Cactospiza pallida, in captivity, selected objects as tools that varied greatly in length, diameter, and flexibility. The shortest tools were hair-like fibers of wood that barely protruded beyond the tip of the beak. The longest was a 20-centimeter "stick" of uncooked spaghetti that one finch probed with briefly (Figure 1). A strong, round applicator stick, about 3 mm in diameter, was the thickest object used as a tool, although one bird held a wooden dowel, 8 mm in diameter, in its beak briefly. The most flexible tools were green pine needles (Figure 2) and thin brass wires, while the most rigid included a section of coping saw blade and an applicator stick.

During our observations, any food that was visible but could not be reached by the beak was the stimulus that most frequently elicited tool-using. A bird would try to obtain a mealworm without a tool and if it failed would use a twig. Quite often, however, a finch picked up a twig when no food was present. Possibly the twigs themselves initiated the behavior. Sometimes the finch picked up a tool at least five or six feet from the crack where it was to be

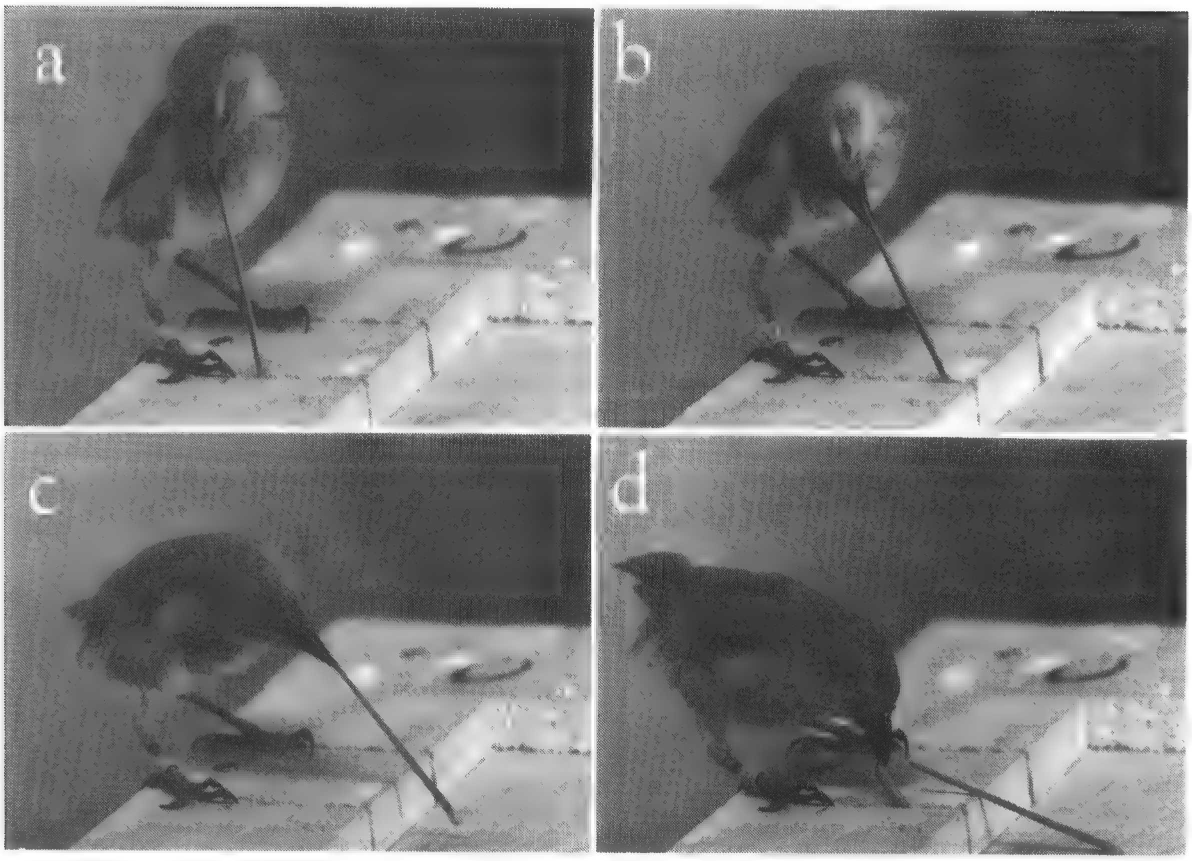

Figure 5. *Cactospiza pallida* using a toothpick tool to dislodge a mealworm from a slot. Note that the finch moves the tool in the direction of the open end of the slot.

used, and carried it, not always in a direct route, to the crack. In one experiment the finches brought tools through a maze, consisting of three overlapping partitions, and deposited the tools near some cracks. Frequently, the birds used tools in cracks that they had not previously explored with their beaks.

Tool-using Movements.—Probing movements were clearly adjusted to the type of tool used. With a very short tool the bird bent forward so that its beak was almost on a level with its feet; with a long tool the bird stood very high and stretched its neck to the utmost. Test birds usually held their tools at one end so that they projected straight in front of the beak. However, they sometimes effectively shortened both long, rigid tools, such as cactus spines and applicator sticks, and flexible tools, such as pine needles and brass wire, by holding them near the middles, which, in the case of flexible objects, gave the tool more rigidity (Figure 3). On one occasion a bird attempted to probe with a 15 cm cactus spine held by one end (Figure 4). Unable to insert the free end of the spine into the crack, even with legs and neck fully extended, and failing to change its hold on the spine to nearer the middle, the bird made a short, semicircular flight and, while on the wing, successfully used the tool to dislodge the mealworm from the crevice. We glued three short sticks together at right angles (Figure 1), and one bird made a number of tries to hold the object in several different places, but it never succeeded in probing with it successfully.

Our birds performed a variety of motions with the tools. Mealworms in cracks were levered sideways (Figure 5) or pulled toward the body; mealworms in transparent tubes were poked through to the far end. At least once a mealworm was slowly levered up the inclined surface of a slippery plastic container in an extraordinary display of motor coordination (Figure 6). One of the most remarkable, and least frequent, behaviors was the use of a tool as a weapon. In one instance, a bird with a probe in its mouth moved toward another bird

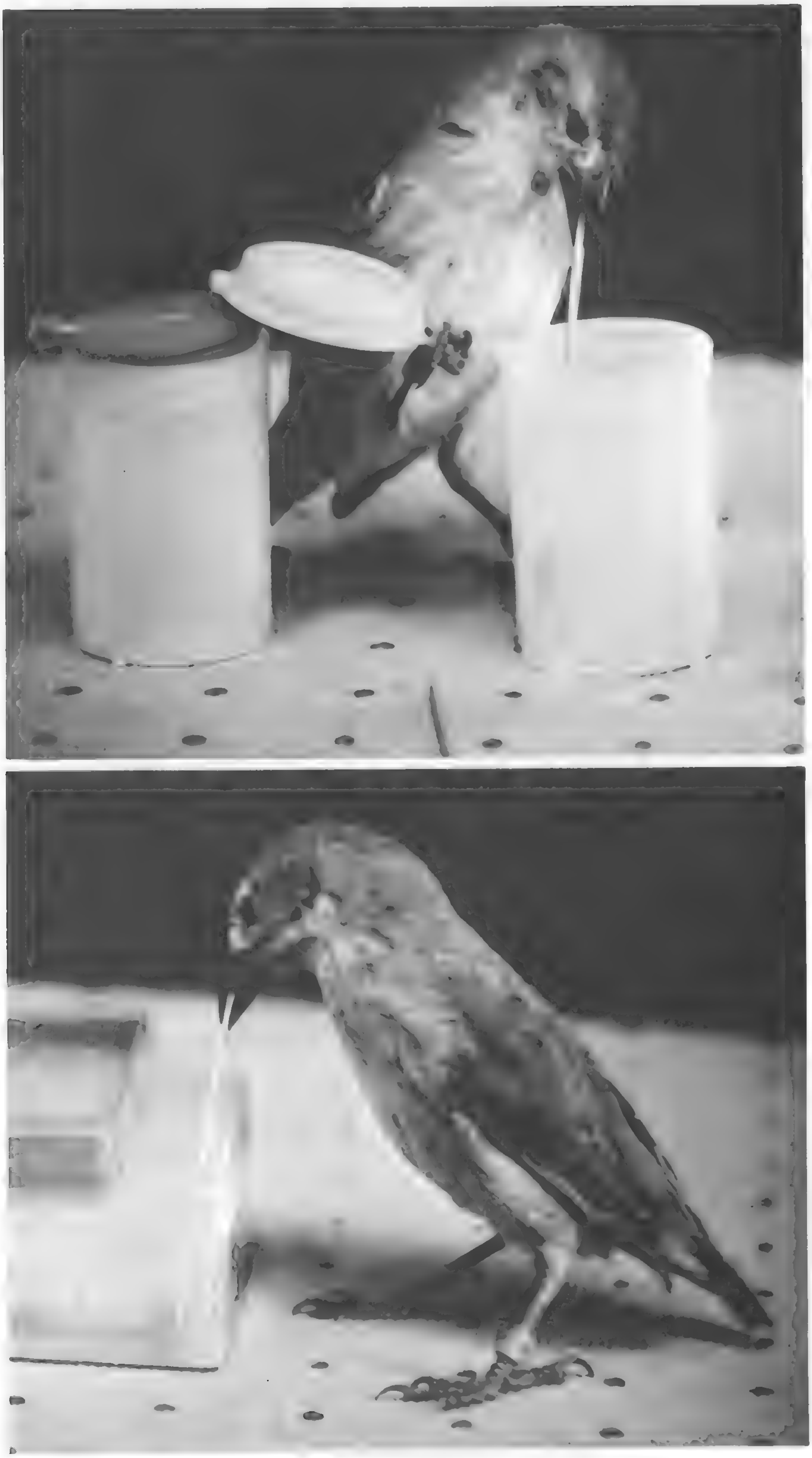

Figure 6. *Cactospiza pallida* from Indefatigable Island, Galápagos, using a wooden applicator stick as a tool. In both examples, the wild-caught finch never attempted to grasp the mealworm directly through the opening of the container. *Above:* the bird persisted for four minutes in unsuccessful efforts to slide a mealworm up the inner wall of the vial and over the rim. *Below:* for shallow holes the bird often used short tools such as toothpicks. Compare with Figure 3.

and drove it from the feeding tray (Figure 7). In another instance, when an unarmed bird, engrossed in foraging at a baited crevice, was suddenly confronted by a weapon-wielding bird, the unarmed bird was more aggressive and forced the armed bird to retreat (Figure 8).

The holes in which our finches probed varied in size. The birds inserted toothpicks into round holes, almost large enough to accommodate their heads, and into cracks barely wide enough for a toothpick (Figure 9). They also inserted twigs into small holes (2 mm in diameter by 10 mm deep) and into the mouths of medium-sized test tubes.

Individual Variation.—Two of our *pallida* showed characteristic styles of tool-using. One bird (58-132523) rarely held a tool under its foot while eating a worm, although the others did so frequently (see Figure 10). Another bird (58-132539) usually flew with a tool to the food tray immediately after picking it up, while the others dropped many twigs before using one.

Of the six birds, one—a male (58-132537)—cocked its head and held food under its feet like the other birds, but we never saw it probe with a twig, even during two periods of intensive observation carried out within an interval of about one year. On looking into its history we discovered that this individual, captured when young, had, unlike the other five, been housed by itself for the three months before it was caged with the tool-using *pallida*. We are unable to conclude that association with experienced birds is necessary for the development of tool-using behavior, since this bird may have suffered another deficiency of experience or inheritance which impaired its performance. If association is important, however, it is apparently maximally effective during a "sensitive" period when the bird is young, since later exposure to experienced birds did not cause the bird to start using a tool.

Controlling Stimuli

We investigated the importance of food in regulating tool-using behavior by manipulating the hunger of *Cactospiza pallida* and the food stimuli to which the birds were exposed.

Hunger.—We observed three *pallida*, individually caged, on four different, though not always consecutive, days. On days one and three, the birds were well fed; on days two and four, they were hungry, having received a limited diet of lettuce and water for at least 24 hours preceding the experiment. At 15-minute intervals we placed mealworms in cracks in a food tray three feet from toothpicks inserted loosely into a stick drilled with holes. We counted the number of toothpicks removed from the stick in a one-hour period starting around 3:00 PM on each observation day.

The data (Table 1) suggest that hunger increases the frequency with which the twigs are picked up. While six paired data represent a small statistical sample, the difference between satiated and hungry birds is significant at the 0.02 level, using the Sign Test. We did not determine definitely whether or not the hungry birds spent more time probing with tools than the other two, but our constant observation during all experimental sessions suggested that they probably did.

Food Stimuli.—*Pallida* frequently inserts twigs into shallow holes where there is no food. Are holes chosen indiscriminately for tool-probing without reinforcement from food stimuli? To test this question, we cut two slots in a block of wood, placed food in one and not in the other, altering the position of the food randomly (Figure 10). We then counted the number of times a

TABLE 1

Number of Toothpicks Removed from a Stick by *Cactospiza* Finches in a One-hour Period

Bird	*Day*	*Number toothpicks removed* *By satiated bird*	*By hungry bird*
58-132523	1	22	—
	2	—	27
	3	11	—
	4	—	19
58-132537	1	5	—
	2	—	16
	3	4	—
	4	—	12
58-132539	1	1	—
	2	—	14
	3	9	—
	4	—	30

tool was inserted in each crack. When the bird raised the tip of the tool above the top of the crack, we considered it withdrawn and counted the next downward thrust as another probe, even if it occurred immediately. The results (Table 2) indicate that the birds showed a preference for cracks containing food, but that some probing occurred in cracks where there was no food.

Functions of Tool-use.—The positive effect of hunger and food stimuli upon tool-using suggests that this behavior represents a significant method of feeding in the wild. The frequent choice of empty slots by hungry birds is puzzling, however. Perhaps, under natural conditions where the contents, if any, of many cracks under the bark of trees may not always be visible, the

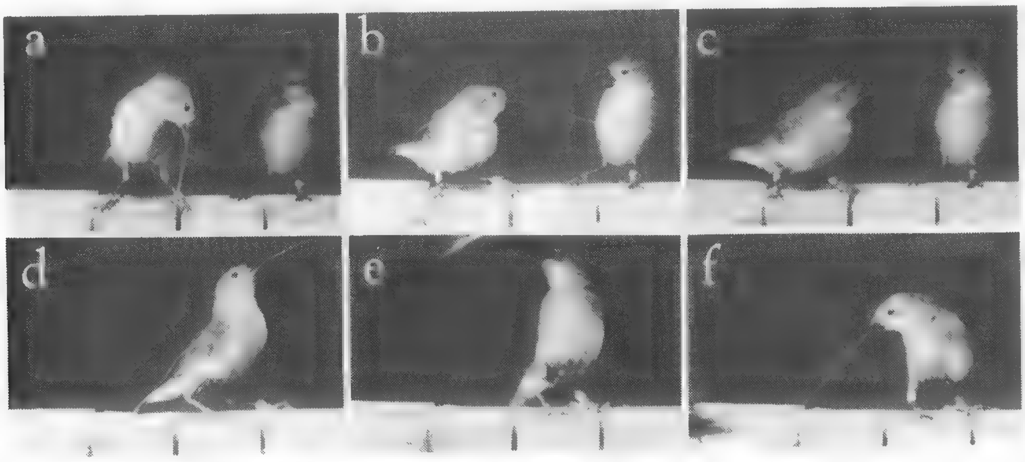

Figure 7. *Cactospiza pallida* using a tool in an aggressive encounter. (*a*) Bird A (left) attempts to remove an insect larva from a crevice using a section of a coping saw blade. Bird B (right) observes passively. (*b*) Bird A swings its head around toward Bird B which gapes. (*c*) Bird A thrusts a tool at breast feathers of B. (*d, e, f*) Bird A follows the flight of Bird B overhead and back to the food table. Enlarged from frames of 16 mm motion-picture film.

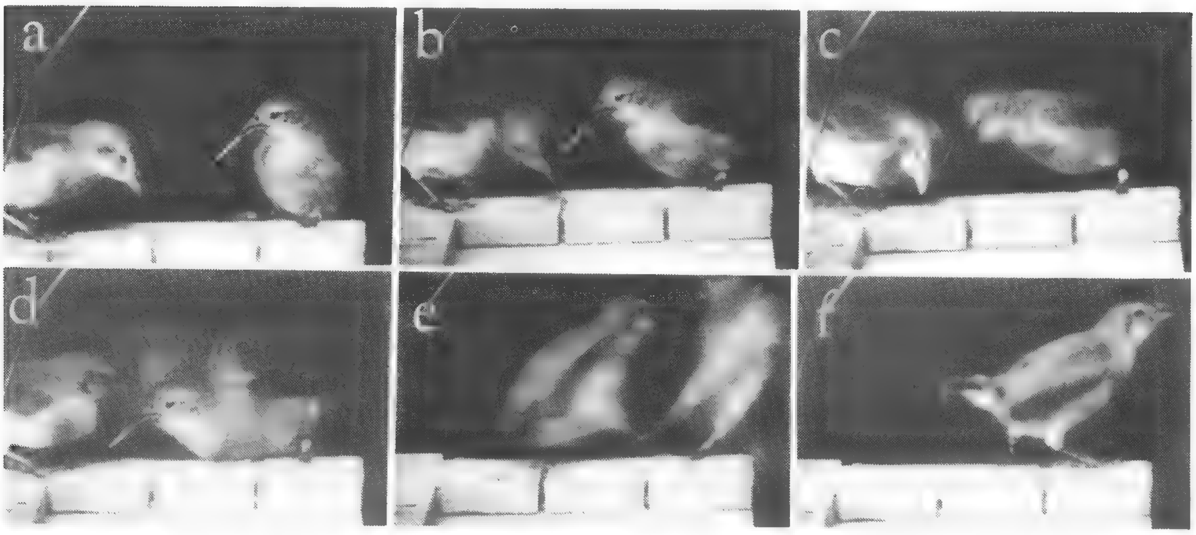

Figure 8. *Cactospiza pallida* using a tool in fighting. (*a*) Bird A (left) approaches the food table where Bird B (right) stands ready to use a tool. (*b*) Bird A peers into a crevice containing a mealworm as Bird B moves forward toward Bird A. (*c*) Bird A turns its head aside as Bird B touches its head with a tool. (*d*) Bird A threatens with bill agape as Bird B prepares to take wing. (*e*) Bird A jumps toward Bird B which now retreats from the food table. (*f*) Bird A, in full possession of the food table, threatens Bird B with gaping bill. Enlarged from frames of 16 mm motion-picture film.

finches use tools to search for food as well as to catch food. Even so, none of our observations on captive or wild birds suggests that *pallida* definitely hunts with a tool; or, in other words, ever picks up a stick before finding a foraging site where the stick might be useful.

Tool-using may also represent a form of displacement activity when another behavioral performance is thwarted in some way. For example, one of our *pallida,* which repeatedly pecked at a mealworm suspended from a string within a glass tube, finally turned to tool-using to capture its prey. Stephen L. Billeb (pers. commun.) supports this view with the observation that tool-use is much more frequent among captive birds than those in the wild.

Manipulative Ability

We compared the manipulative ability of *Cactospiza pallida* with that of other captive Galápagos finches and some species of American continental songbirds, using two measures: (1) the appearance of movements judged to represent incipient tool-use, and (2) the achievement of mastery in a string-pulling task.

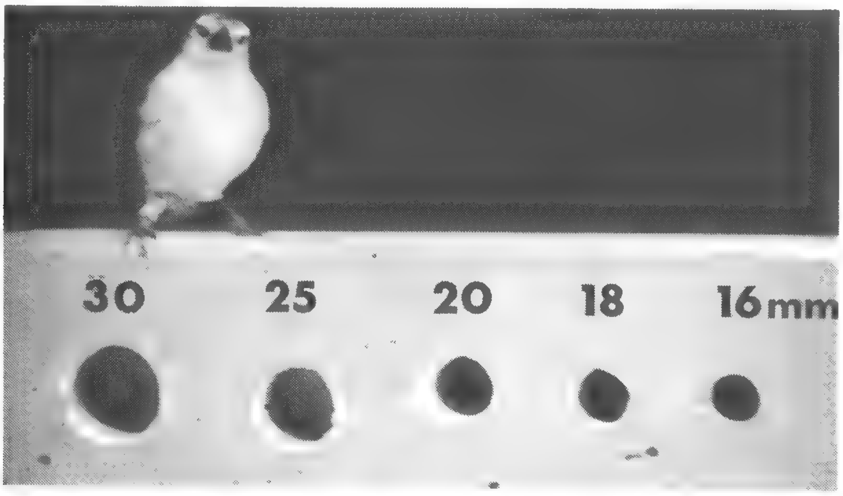

Figure 9. Device used to determine the size of holes into which *Cactospiza pallida* would insert its head to obtain mealworms. The wooden block is on its side.

TABLE 2

Number of Probes by *Cactospiza* Finches into Slots with and without Food

Bird	*Baited slot*	*Unbaited slot*
58-132504	47	1
58-132523	29	9

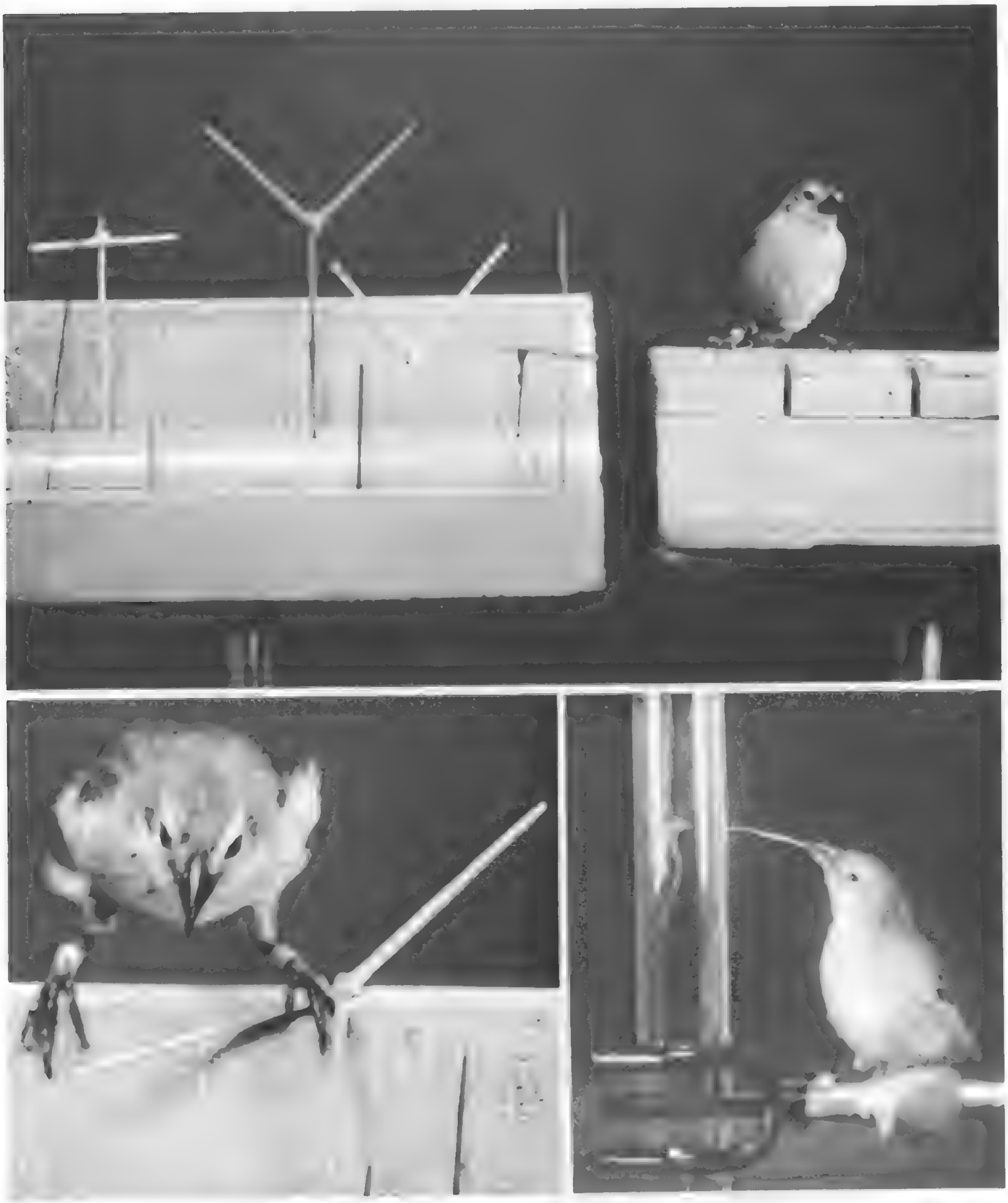

Figure 10. *Above:* arrangement of tool shelf and food table used in experiments described in the text. *Below* (left): *Cactospiza pallida* demonstrating the use of the foot to hold objects, in this case a Y-shaped tool. *Below* (right): *Cactospiza pallida* "tooling" at a mealworm which is suspended from a string within a glass tube.

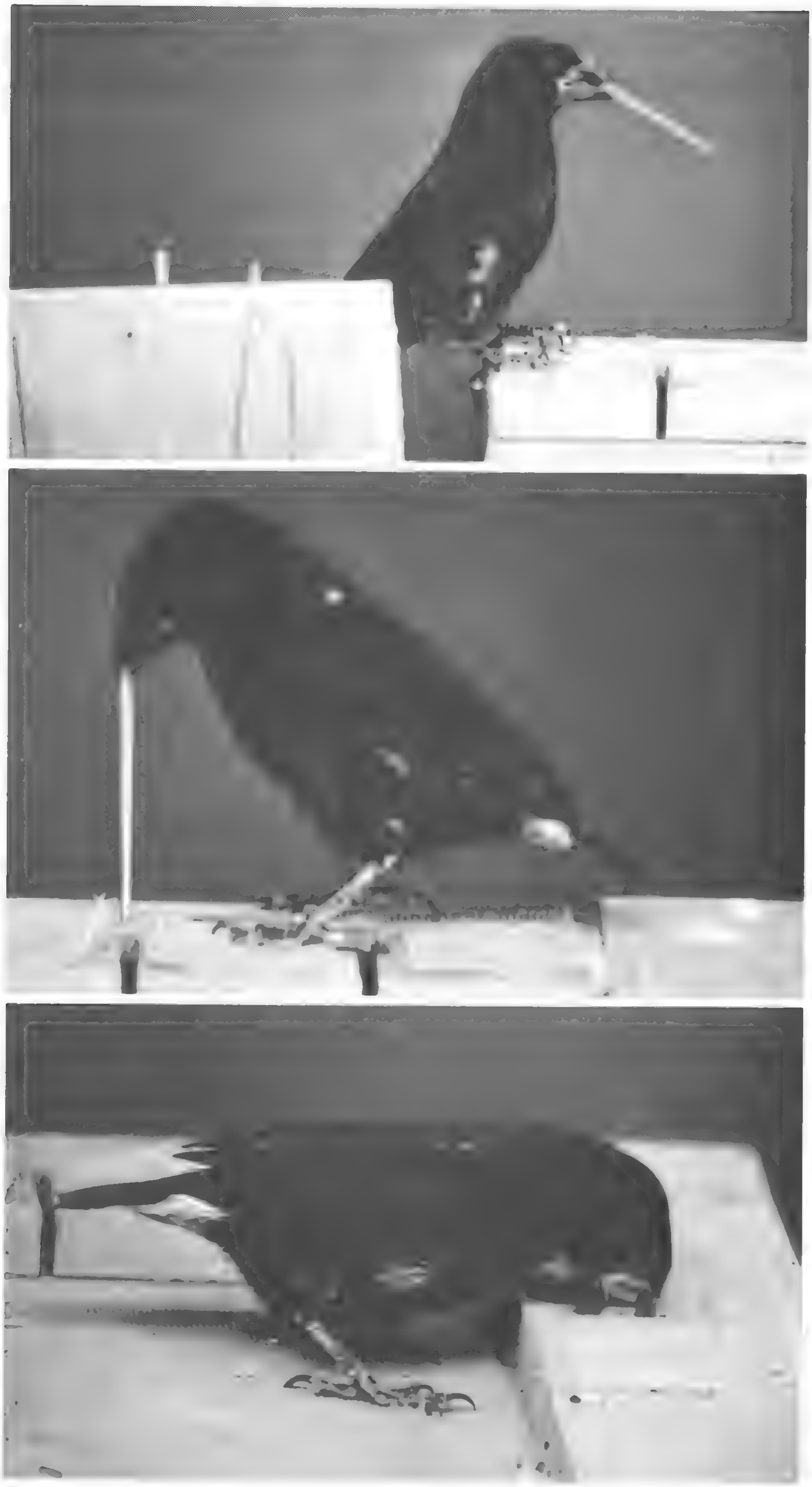

Figure 11. *Top:* a short wooden stick in the bill of *Geospiza conirostris* is atypical of this species. *Center:* this individual sometimes used a stick to probe into unbaited crevices but rarely, if ever, into baited ones. *Bottom:* the same bird has inserted its bill into a narrow crevice containing a mealworm. With bill agape and tongue protruding, the bird was trying to move the worm to within reach of the open mandibles. The laterally compressed bill, typical of this species of *Geospiza,* allows for deep probing of narrow slots.

TABLE 3

Results of String-pulling Tests on Darwin's Finches and Some American Songbirds

Group	*Species*	*String-pulling*
Darwin's Finches	*Cactospiza pallida*	+
	Camarhynchus psittacula	+
	Camarhynchus pauper	+
	Camarhynchus parvulus	+
	Geospiza conirostris	+
	Platyspiza crassirostris	–
	Pinaroloxias inornata (Cocos Island)	–
American songbirds	Plain Titmouse* *(Parus inornatus)*	+
	Mockingbird* *(Mimus polyglottos)*	–
	Loggerhead Shrike* *(Lanius ludovicianus)*	+**
	Red-winged Blackbird* *(Agelaius phoeniceus)*	–
	Brewer's Blackbird* *(Euphagus cyanocephalus)*	–
	Cuban Grassquit *(Tiaris canora)*	–
	White-crowned Sparrow* *(Zonotrichia leucophrys)*	–

*Hand-reared individuals.

**String-pulling in this species did not involve the coordinate use of bill and feet. The bird obtained the pendant larva by pulling on the base of the string, thus causing the hanging portion to slip under the hooked end of the upper bill like a pulley. See Figure 14.

Incipient Tool-use.—Despite attempts to teach tool-use to other species of finches from the Galápagos by caging them with *pallida,* we saw the behavior in only one bird—a male *Geospiza conirostris* from Hood Island, which not only picked up twigs, but also stuck them in cracks (Figure 11). This bird, captured in March 1962, while in a plumage indicative of more than one year of age (i.e., Stage Number 3, Bowman, 1961) lived for the following year in a flight cage adjacent to a cage containing two adult *Cactospiza pallida.* During this year we often saw *pallida* pass sticks into the adjacent cage where *G. conirostris* picked them up with its bill. We assume that this *conirostris* learned to manipulate sticks from its neighbors. Another Galápagos finch, *Certhidea olivacea,* was once observed in the wild holding a three-inch leaf petiole with which it probed into a crack three times (Hundley, 1963). The only report we have found of twig-probing in a non-Galápagos bird, and one which Chisholm (1954) regards as "possibly faulty," is a single observation of an Australian bee-eater, *Merops ornata,* using a twig as a mining tool.

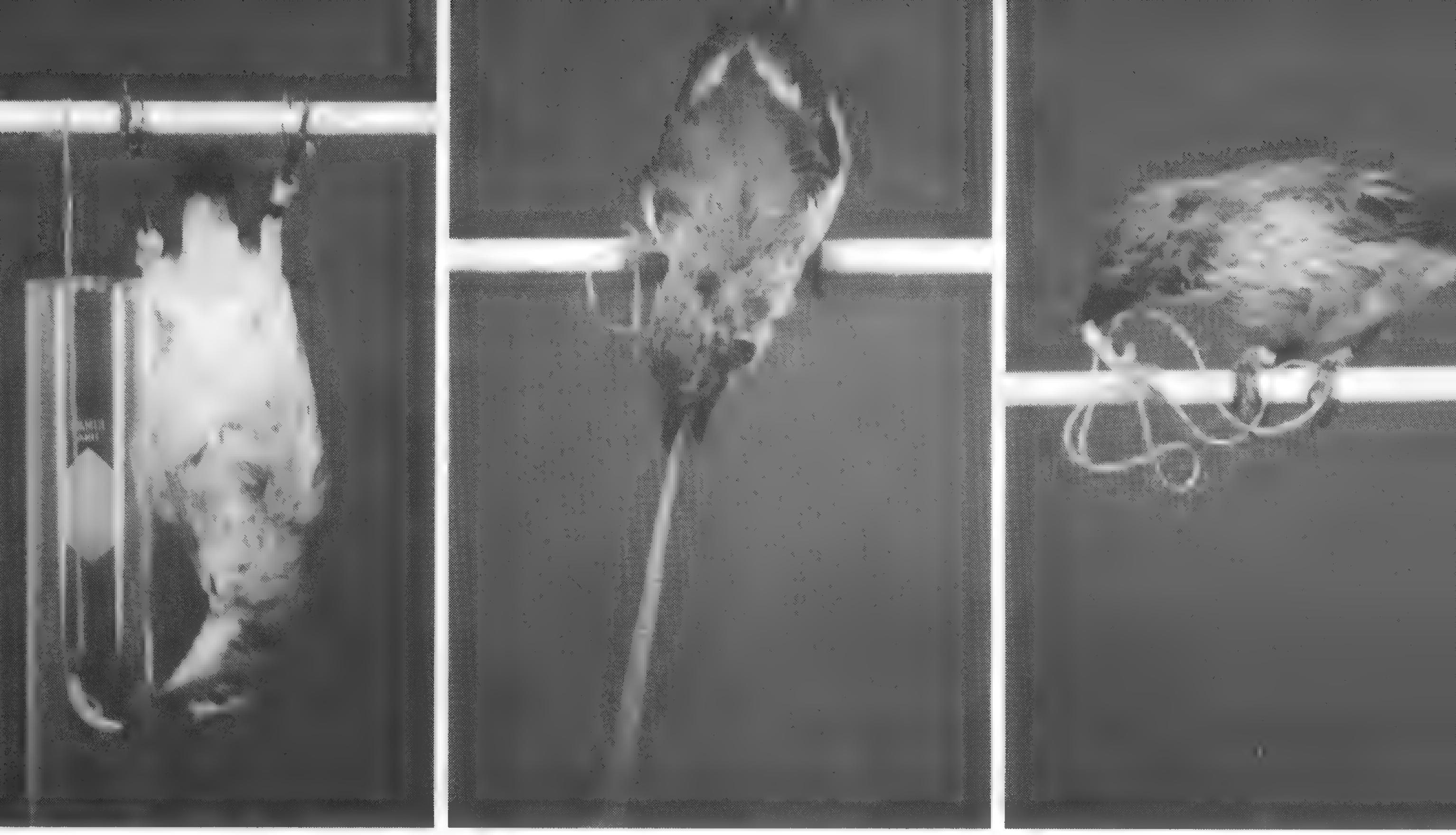

Figure 12. *Cactospiza pallida* reacting to a mealworm suspended on the end of a string. *Left:* the finch hangs upside down from its perch, its legs fully distended, and pecks at a mealworm enclosed in a glass tube (cf. Figure 10, lower right). *Center:* holding several loops under its toes, the bird prepares to take a new bite on the hanging string. *Right:* the bird has just succeeded in reaching the mealworm by pulling up the last portion of the eight-inch-long string.

Searching movements, comparable to those of *Cactospiza pallida* occur in many insectivorous mainland species, including warblers and titmice; and on the Galápagos similar searching behavior occurs in three species of *Camarhynchus* and in the *Certhidea* finches.

String-pulling.—In this experiment we used North American birds, which had been hand-reared and presented no problems with fear reactions, and Galápagos birds which, although they had been wild-trapped, generally showed less fear of humans than the wild North American species and acclimatized to the testing chamber in one or two days. We tied a mealworm to the end of a string and held it below a wooden perch far enough to prevent the bird from reaching down and biting it. Sometimes we shielded the worm by a glass tube (Figure 12).

Table 3 shows that some species of both of these groups can learn string-pulling. Thorpe (1956) reports that several European species can do likewise. Interestingly, the *Cactospiza* finches were not the best string-pullers. The Plain Titmouse (*Parus inornatus*) and species of *Camarhynchus* learned the task faster and pulled up longer strings (see Figures 13 and 14). However, *Cactospiza pallida* tried to get the worm in more ways than the others. It flew up to the pendant worm from below and hung onto it by one foot; it poked twigs at it (Figure 10). The greater success of the Plain Titmouse and *Camarhynchus* sp. appeared to be due to a stronger tendency to peck at the string and a greater facility in holding the string with the feet (Figure 15). Clearly different kinds of manipulative ability exist in birds but there is probably an overlap between abilities. Tool-using and string-pulling both require a seizure of inanimate objects by the beak and a sustained coordination of head movements with visual information.

Origin.—As a group, the Galápagos finches do not appear to possess a startlingly greater capability for manipulative behavior than several groups of continental birds. The Galápagos finches pulled string no more readily

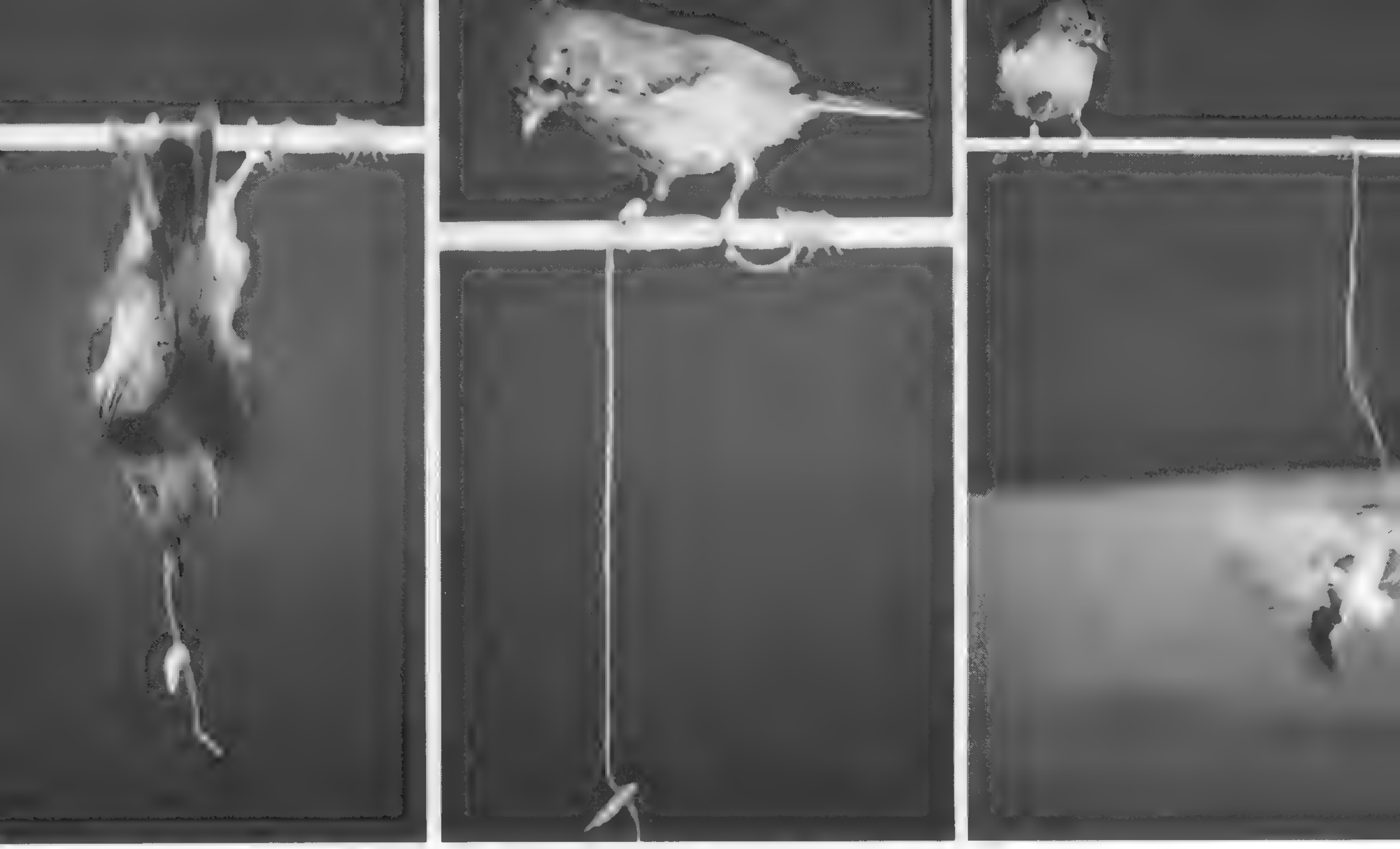

Figure 13. Reactions of a hand-reared Plain Titmouse to a mealworm suspended on the end of a string. *Left:* the titmouse hangs upside down from its perch, legs fully distended, attempting to reach a larva with its bill (cf. *Cactospiza pallida,* Figure 12, left). *Center:* the titmouse holds under both feet a short loop of string that it pulled up to the perch with its bill. *Right:* occasionally, the titmouse attempted to seize the worm directly with its bill while in flight.

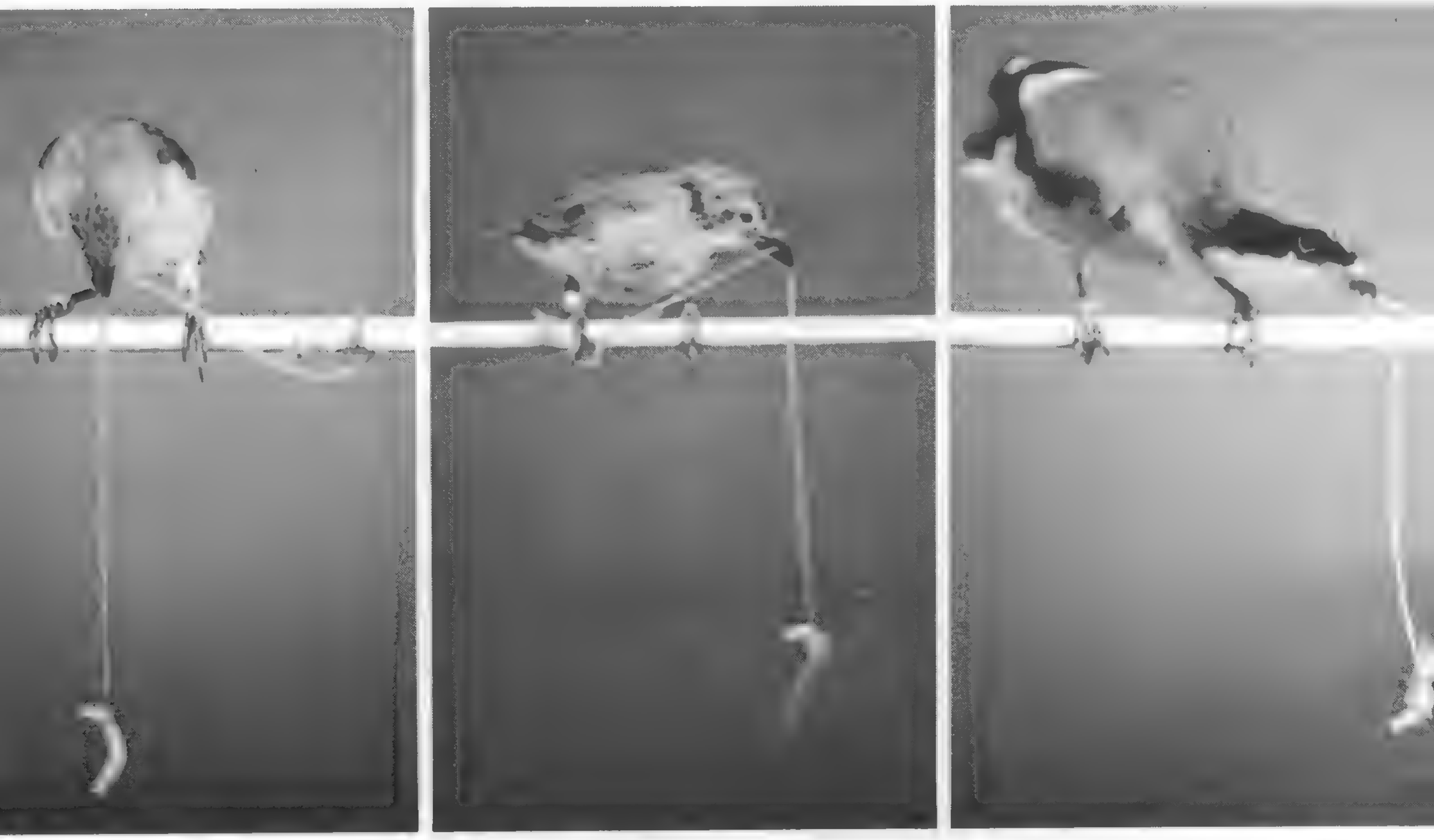

Figure 14. String pulling by two species of Galápagos finches and a Loggerhead Shrike. Wild-caught individuals of *Camarhynchus psittacula* (*left*) and *Cactospiza pallida* (*center*) show a basically similar neuromuscular coordination of bill and feet in string-pulling behavior. Without using its feet, a hand-reared shrike (*right*) obtained the suspended larva by pulling on the base of the string, causing the pendant portion to slip under the hooked end of the upper bill.

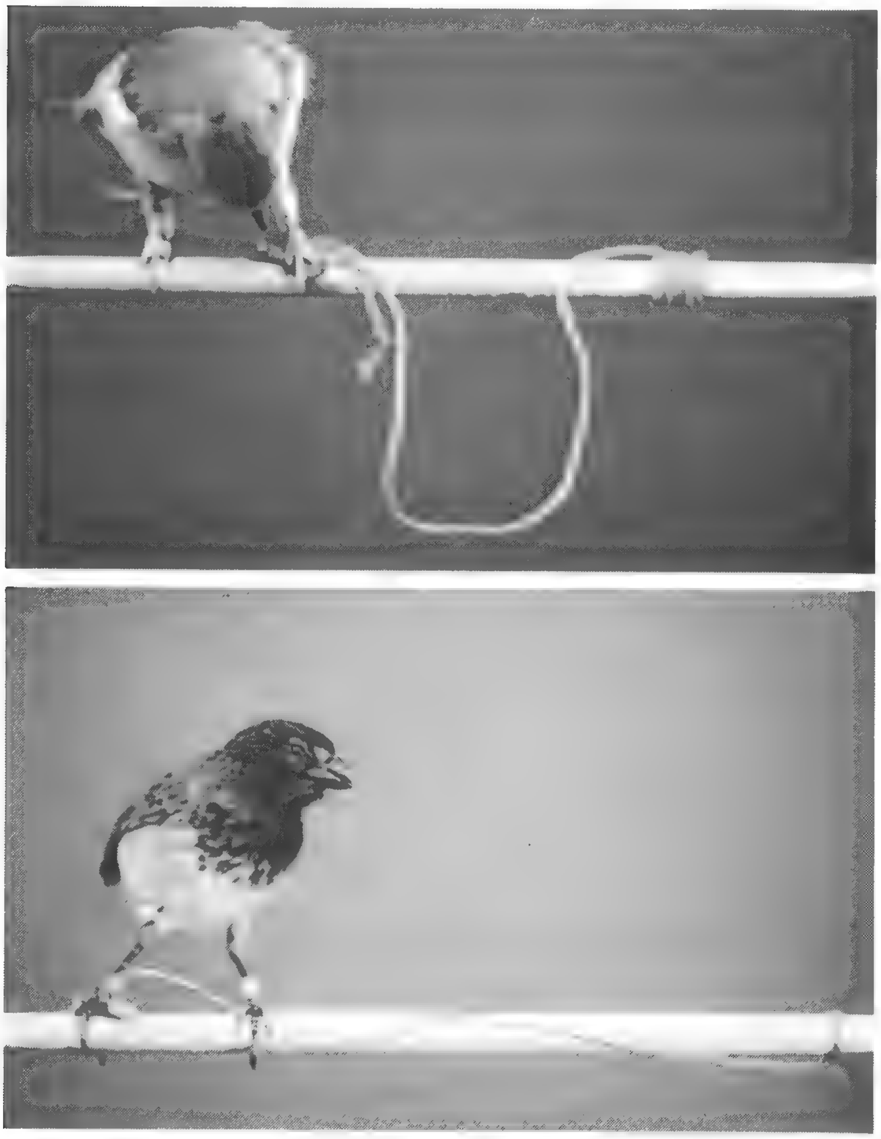

Figure 15. The Plain Titmouse (*above*) of western United States and *Camarhynchus parvulus* (*below*) of the Galápagos Islands are ecological and behavioral equivalents. Here both species are shown after sidling along the perch. The mealworm, obtained by string-pulling, is held with one foot during feeding.

or efficiently than, for instance, the North American Plain Titmouse. Perhaps incipient tool-use occurs only in the Galápagos birds, but the data are too scanty to make comparisons. The failure of tool-using to evolve in parts of the world other than the Galápagos Islands cannot apparently be explained by any unique genetic feature among the assemblage of Galápagos finches.

Ecological factors were probably more important in the evolution of tool-using in *Cactospiza pallida*. The dry climate which prevails in the Galápagos throughout most of the year causes insects, especially lepidopterous and coleopterous forms, to hide beneath bark or to burrow into woody tissues during the daylight hours when *pallida* is foraging. Tool-using may, therefore, be more advantageous in the Galápagos than in places with a moister climate. Lack (1947) suggested that "Had a small American woodpecker been established in the Galápagos, it is most unlikely that the Woodpecker Finch could ever have evolved." The point is well taken although it seems possible that a tropical tanager might have presented more serious competition for the finches, since many tanagers feed extensively on insects living in rotting wood as well as on fruits. In this they resemble *Cactospiza pallida* and differ from American woodpeckers (see Skutch, 1954). We agree with Lack (*op. cit.*) that there appears to be nothing in the manner of manipulation of nest materials that would tend to promote tool-use.

Summary

Cactospiza pallida, a finch from the Galápagos Islands, uses many alternative movements when obtaining insects with a twig, and some individuals show characteristic styles of tool-using.

Hungry *pallida* use more tools than *pallida* not deprived of food and probe more frequently into food-filled cracks than into empty cracks. We suggest that tool-using probably represents a significant method of feeding in the natural environment and may be used not only to catch insects but also to find them when they are hidden in deep crevices.

Manipulative ability of *pallida* is not noticeably greater than that of certain North American mainland birds. We suggest that ecological, and not genetic, factors best explain the unique occurrence of twig-probing in the finches of the Galápagos Islands.

Acknowledgments

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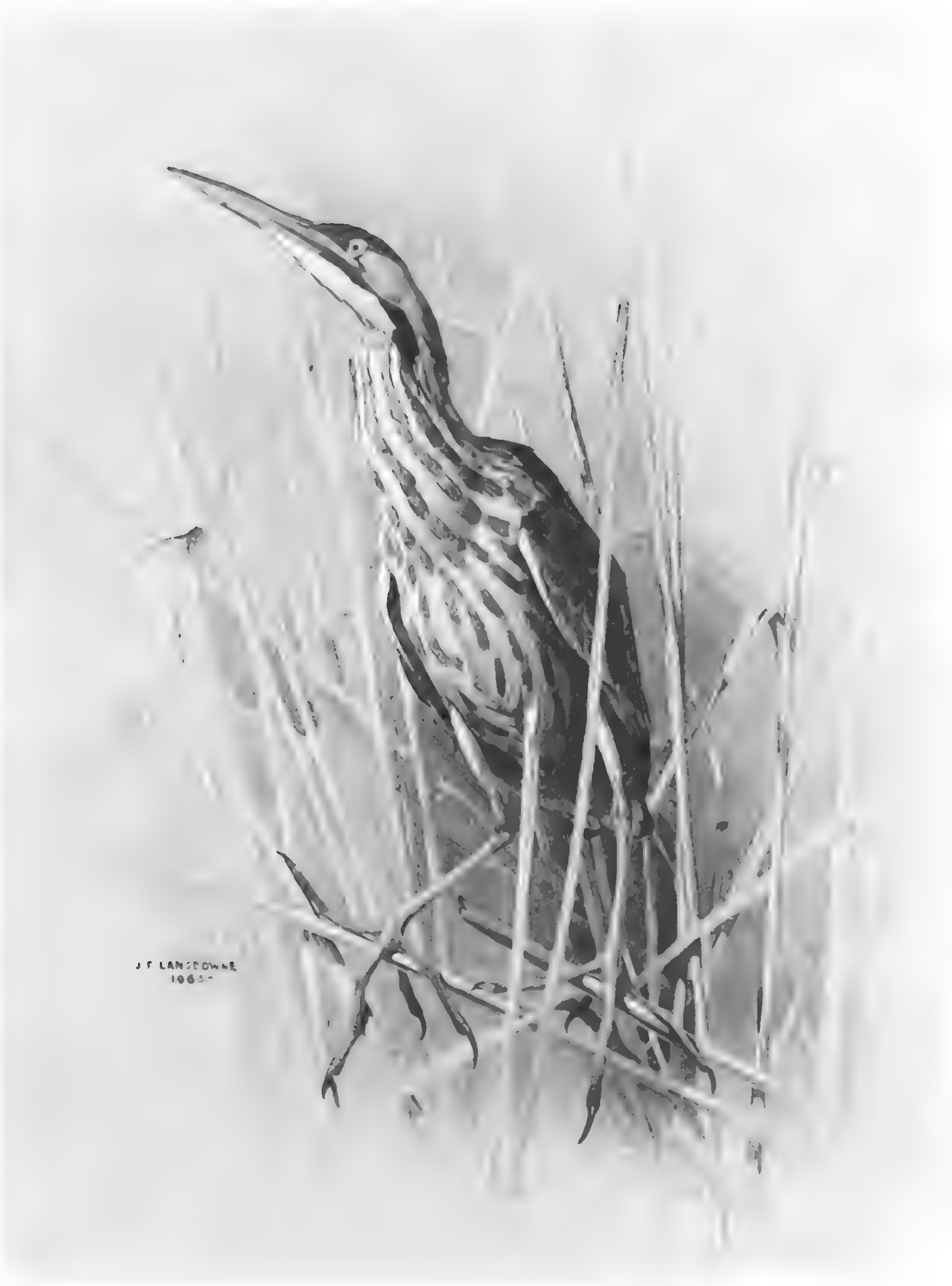
J F LANSDOWNE
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American Bittern, *Botaurus lentiginosus*. Painting by J. F. Lansdowne.

ECOLOGICAL AND BEHAVIORAL ASPECTS OF PREDATION BY THE NORTHERN SHRIKE

Tom J. Cade

The predatory mode of existence has been an often repeated theme during the course of evolution. From the slimy hagfish, that insidiously squirms its way through the mouth of its prey and then literally eats the fish from the inside outward, to the great cats with their highly specialized carnassial teeth and their retractile claws, no class of vertebrates is without some members which get their living primarily at the expense of other vertebrate life. Although there are many kinds of predators—generalized feeders as well as specialists—perhaps the most exciting to the human mind are those which kill and eat other species closely related to themselves. Haunted as we human beings are by our own vestigial inclinations to pursue quarry, mammalian predators on other mammals and avian predators on birds somehow seem more predatory to us than those which eat animals far different from themselves phylogenetically.

The diurnal birds of prey (Falconiformes) and the nocturnal birds of prey (Strigiformes) are the most familiar predators among birds, but many other avian orders contain species that have become adapted in one way or another for a diet of flesh. The large and diverse order of perching birds (Passeriformes) contains one family—the shrikes or Laniidae—many species of which live by killing small reptiles, birds, and mammals, as well as insects. Although very hawk-like in their habits, the shrikes are actually more closely related to such familiar songsters as robins, thrushes, warblers, and others.

The true shrikes, or butcherbirds of the genus *Lanius,* get their Latin name from their habit of impaling prey on a thorn or in the forks of a branchlet. Often, an individual shrike favors certain trees or bushes for this purpose so that a number of carcasses may be hung in the same tree or grove. Such a place is called a "larder" and is reminiscent of the way butchers used to hang up their meat on hooks in the open street markets of ancient Rome. Thus the name *Lanius,* or butcher, was applied to these birds long before our present system of scientific nomenclature came into existence.

One of the largest species is the Northern Shrike (*Lanius excubitor*), more appropriately called Great Grey Shrike in Britain. The species name, *excubitor,* means watchman or sentinel, so that a literal translation of the full Latin binomen can be given as "the watchful butcher," an apt name for this capable and alert little predator. In its territory the shrike habitually perches—exposed—atop one of the tallest trees from which it keeps a constant watch for quarry moving below, as well as for attackers from above, for the shrike itself is often pursued by hawks.

When a hawk passes over, the shrike utters a shrill whistle and plummets straight down among the densest branches of its tree—emerging only after the hawk has disappeared. Small accipiters and falcons appear to be its worst enemies. In the Old World this species' alertness in spotting hawks has long been known to falconers and hawk trappers, who used to use a tethered butcherbird to signal the presence of a passage falcon approaching the trapping area (see Michell, 1900, for details).

Most of the time, as it sits fluffed out in a lollypop-like silhouette surveying its world, the Northern Shrike is rather an innocuous looking bird. Often quite tame and unsuspicious even in the wildest regions, it sometimes sings a feeble though not unpleasing song—utterly belying its true nature, which it is ready to reveal the instant a mouse or small bird moves within its sphere of attack.

During the breeding seasons of 1952 and 1956 through 1963, I observed Northern Shrikes at 27 nests in arctic Alaska. One of the nests was along the Steese Highway north of Fairbanks; the others were along the Colville River, between the mouths of the Etivluk and Umiat, and at Lake Peters on the north side of the Brooks Range in the vicinity of Mount Michelson. Since shrikes commonly hunt around their nests and can easily be seen carrying, impaling, and feeding on their prey, I had no difficulty finding more than 200 carcasses hung up in their larders, and collecting for analysis more than 500 regurgitated pellets around their nests. Besides my observations in Alaska, I have watched Northern Shrikes hunt on their wintering grounds around Syracuse, New York, and I have kept 21 Northern Shrikes in confinement for close studies of their behavior. Four of these captive birds I trained by the methods of falconry to fly free out-of-doors, to hunt, and to return on call to a portable cage.

The information obtained by these various techniques allows for a thorough description of the hunting behavior of the Northern Shrike and for an analysis of the ecological significance of predation by shrikes in arctic Alaska. I have organized the presentation and discussion of this information around a series of questions that one always asks about any predator. Where do shrikes live? How do shrikes hunt? How do shrikes kill their prey? How do shrikes eat their food? What kinds of animals do shrikes eat? How much do shrikes eat? Do shrikes exert a regulatory influence on the distribution and numbers of their prey? What factors control the numbers of shrikes? These questions deal in part with such fundamental areas of biology as (1) adaptation and evolution of behavior, (2) bioenergetics and energy flow through an ecosystem, and (3) population dynamics.

Distribution and Habitat of the Northern Shrike

The Northern Shrike is a bird of panboreal distribution, breeding across the northern parts of North America and throughout much of Eurasia. Certain races even extend their ranges into North Africa. In North America, the center of its breeding distribution lies in the broad belt of coniferous forest, or taiga, which stretches across Canada and Alaska. Even so, the Northern Shrike is not characteristically associated with continuous stands of conifers since it shows a strong preference for the forest edge.

In interior Alaska, for instance, between the Brooks and Alaska Ranges, shrikes are to apt to occur in the spruce-birch forest wherever there are open-

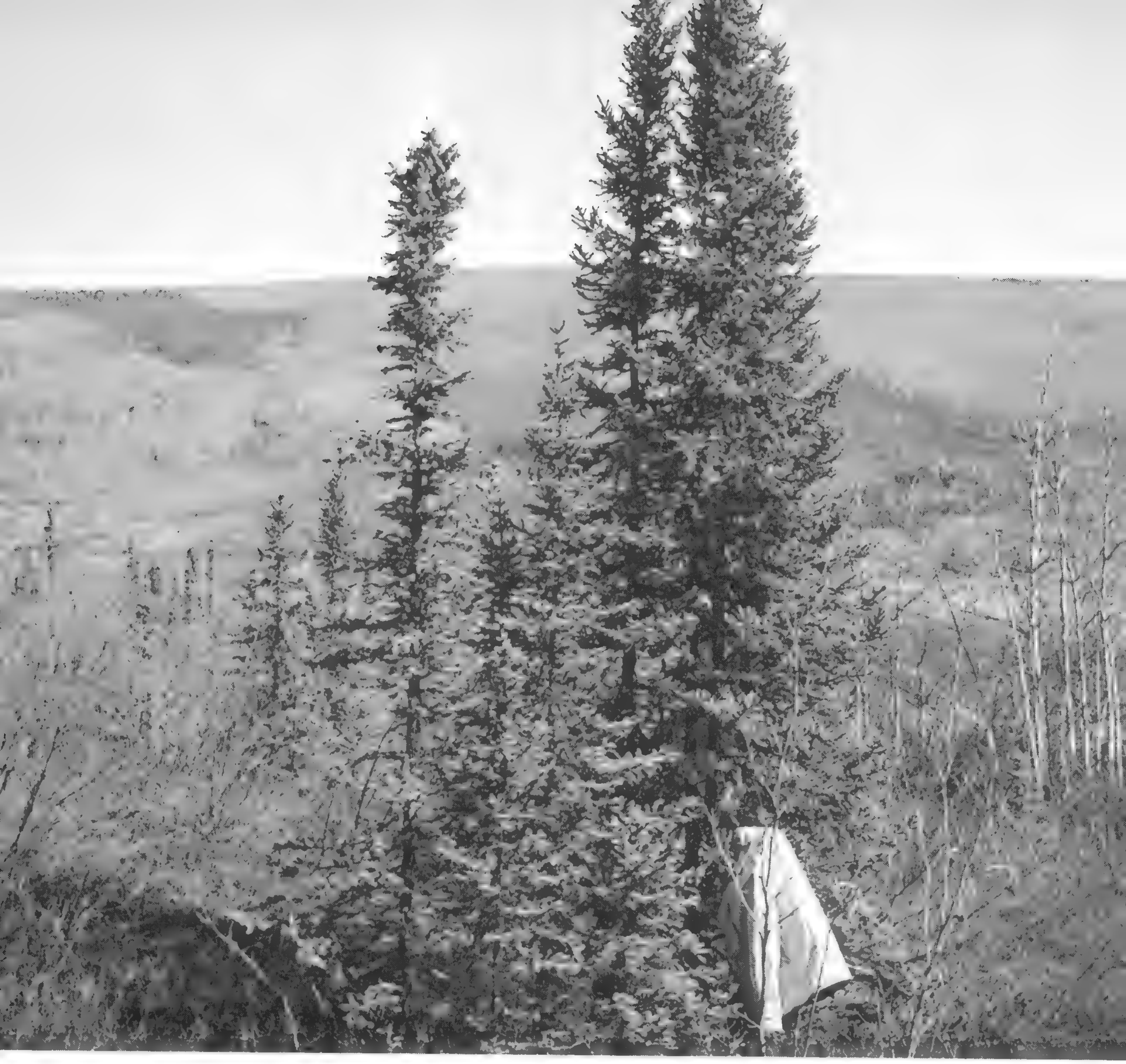

Figure 1. Nesting habitat of the Northern Shrike in a black spruce bog along the Steese Highway, 25 miles north of Fairbanks, Alaska, May 1957. The nest was situated about 10 feet up in a group of four 15-foot-high black spruce poles.

ings such as along a river, around a lake, or a burned area, muskeg, or black spruce bog; but nesting is especially noticeable at the altitudinal and latitudinal limits of the spruce forest, as in Mount McKinley National Park (Dixon, 1938; Murie, 1946) and in Anaktuvuk Pass in the Brooks Range (Irving, 1960). The altitudinal limit of spruce is reached at elevations of 2,500 to 3,000 feet in the Alaska Range, and the latitudinal limit roughly follows the main divide of the Brooks Range in the north where undoubtedly altitude is also an influence. In such regions, the shrikes tend to place their nests in brushy growths of black spruce, willow, or alder rather than in the mature white spruce trees. Figure 1 shows nesting habitat in a black spruce bog north of Fairbanks, Alaska.

Because of its predilection for a semiopen landscape and for brush-like vegetation, the Northern Shrike has been able to establish a breeding population on a portion of the Arctic Slope of Alaska far beyond the northern limits of the spruce. In northern Alaska, shrikes are entirely restricted to streambed situations in the foothills where conditions support stands of willow and alder four or more feet high. Such stands occur along all the major rivers and their tributaries in the foothill tundra; and I have had most of my experience with

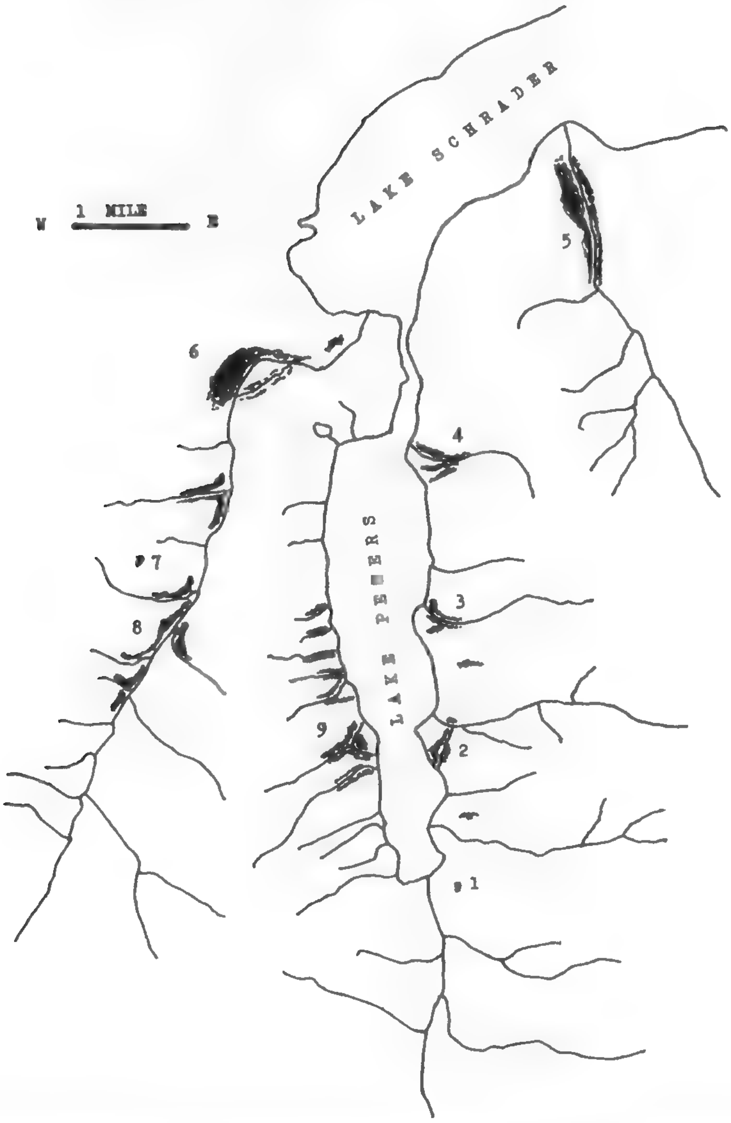

Figure 2. Distribution of nesting areas and nesting habitat of the Northern Shrike around Lake Peters and Lake Schrader, Brooks Range, Alaska. The numbers indicate locations used by nesting shrikes one or more times between 1958 and 1963. The black areas show the approximate extent and distribution of willow brush four or more feet high.

nesting shrikes along the Colville River, which is the principal drainage of the Arctic Slope, and in the vicinity of Lake Peters, which lies in a deep valley on the north front of the Brooks Range.

The dependence of breeding shrikes on stands of willow brush in northern Alaska is illustrated by the history and distribution of nesting sites around Lake Peters from 1958 through 1963 (Figure 2). In this region, willows—mostly felt-leaf willow—grow in isolated, small stands, about four to 15 feet in height, along the creeks and drainages cutting down through the alluvial fans to Lake Peters and Lake Schrader. There are approximately 21 separate stands of willow growing in the region depicted in Figure 2, and the shrikes used nine of these as nesting habitat 19 times between 1959 and 1963; in addition, there were six old nests in 1959 dating from the previous year or two. In general, the larger stands were the ones most frequently used, although the shrikes used the large Area 6 only once, while they used Area 1, consisting of a small, low stand of green-leaf willow, twice. Figures 3, 4, and 5 show typical nesting trees and habitat around Lake Peters.

Although the Northern Shrike is somewhat migratory in North America, even in winter it does not extend its range very far south. Some individuals overwinter within the breeding range, while others move south as far as the northern tier of states—somewhat farther south in some years.

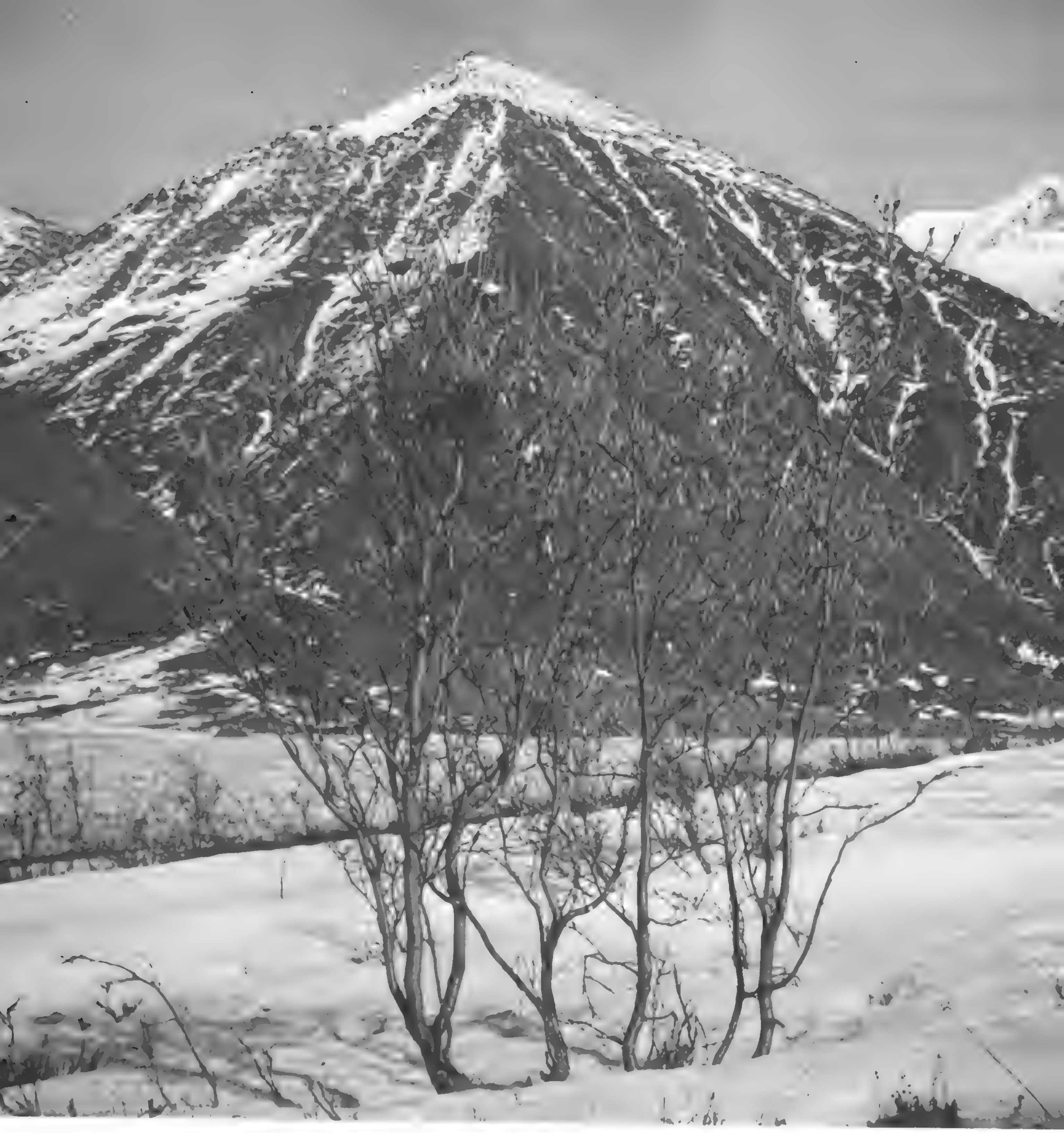

Figure 3. Shrike nest eight feet up in a felt-leaf willow, in Area 9 at Lake Peters, late May 1959. The alluvial fan of Area 2 shows up in the background across the lake. Refer to Figure 2 for locations.

Hunting Behavior

Hawking with Shrikes

Much of what I know about the hunting tactics of the Northern Shrike has been gained by close observation of trained shrikes. Elsewhere I have described in detail some of my early experiences hunting with shrikes (Cade, 1962), and my later work with these birds has generally confirmed the conclusions reached at that time.

A hand-reared shrike is easily trained to accept a portable cage of moderate dimensions as its home (Figure 6). If it is always fed inside the cage, and particularly if it is provided with a spike or other device for impaling, the shrike quickly learns to associate the cage with food, and, when released outdoors in a hungry state, will return and fly into it from several hundred yards away. When the shrike has captured quarry, if the cage can be set down on

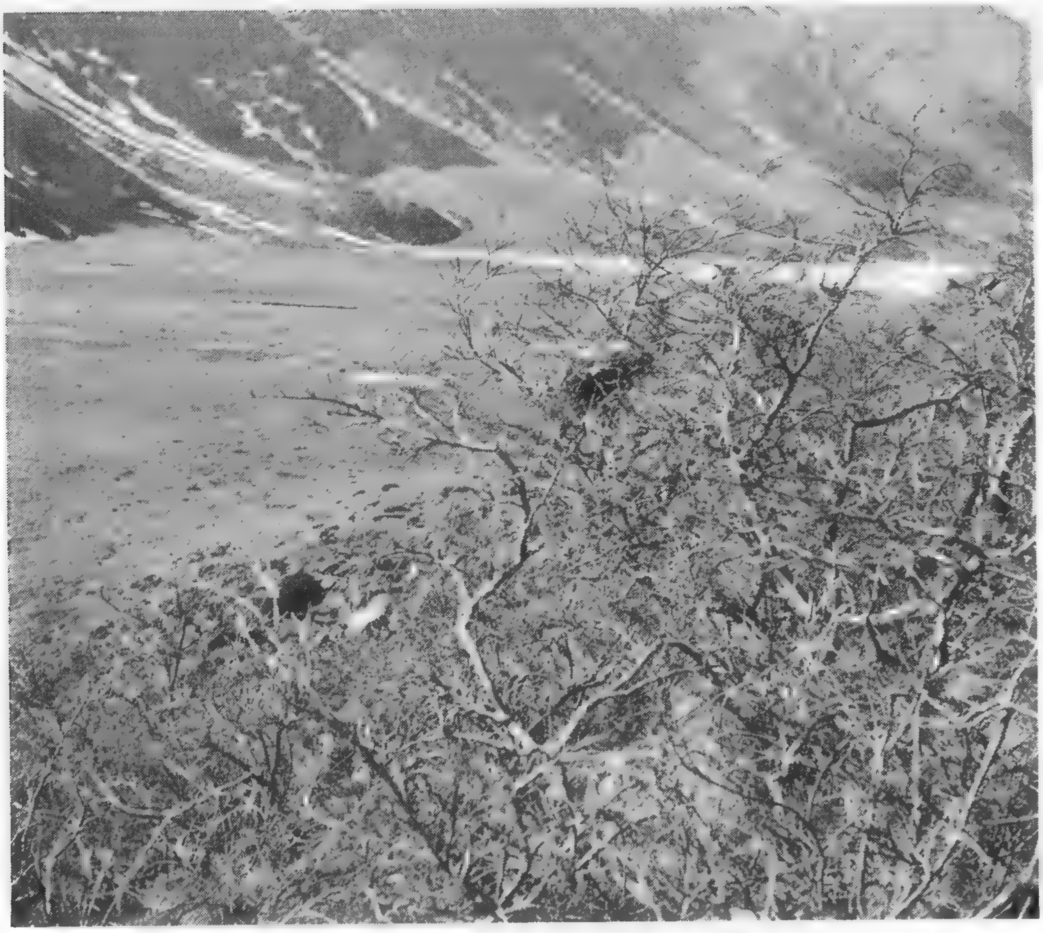

Figure 4. Shrike nest three and one-half feet up in a green-leaf willow with a crown of five feet, situated on the side of a lateral moraine, June 1959. The south end of Lake Peters is in the background.

the ground nearby before the bird flies off with its booty, the shrike will usually carry its prey into the cage and impale it on the familiar spike. Otherwise, the shrike will fly off with its prey and impale it on some natural spike or fork, usually well out of human reach. Fortunately, once the prey is secured, the trained shrike will leave its food cached in the tree and return to the cage for a tidbit of meat. I have never lost a trained shrike permanently by hunting with it, a statement that I cannot make about hawks and falcons.

Hawking with a trained shrike can be quite as exciting and informative as hunting with a hawk or falcon, but only a few falconers have tried this sport. According to Charles D'Arcussia (see Michell, 1900), among the many hawking establishments kept by King Louis XIII of France was one for shrikes, which were trained to fly at small birds. He relates a quaint story about one of the king's butcherbirds that would fly up to a heron on the wing and whisper in his ear. Husāmud-Dwalah Taymūr Mirza, author of a Persian treatise on falconry written in 1868, mentions that shrikes were trained in the Near East to catch small birds; and this practice was evidently also indulged from time to time in the northwestern districts of India (Phillott, 1908). Marrash (1956) is the only modern falconer who seems to have written about training shrikes. He used the traditional method of employing a leash and jesses for restraining his bird, a wild caught adult, which he flew around Khartoum. I have found these trappings much too encumbering for a bird as small as a shrike, and my technique of using a portable carrying cage is much less restrictive and damaging to the bird.

Usually on reaching the hunting grounds, I simply let the shrike out of its cage and then followed it, recording its various activities. Occasionally, I stalked quarry by getting as close as I could first with the shrike in its cage, and then released it as the prey took flight. The following episodes give an idea of the kinds of behavior that I observed during hunts with a trained shrike.

Observations

29 December 1960, 10:00 AM, Manlius, New York.—"Green," an immature shrike weighing 70 grams, was perched atop a tree about 25 feet off the ground in my backyard. I released an adult male House Sparrow (*Passer domesticus*) at a distance of 30 feet from the shrike. The shrike immediately gave chase, and the sparrow flew into a cedar bush 40 yards away. The shrike went into the shrub after the sparrow, and in a few seconds the sparrow flew out and away into an elm tree some 100 yards from the cedar bush. The shrike followed close behind the sparrow but then swerved off at the last moment to perch near the top of an adjacent elm. The sparrow "froze" to a perch in the center of the elm. The shrike sat quietly for about 15 seconds, looking intently down toward the sparrow, and then suddenly dived into the other tree and grabbed the sparrow in its feet before the prey moved off its branch. Green carried the sparrow to the ground and killed it there, after which she impaled it in a cedar bush.

29 May 1961, 3:30 PM, Barrow, Alaska.—I released Green—now one year old—to fly at will in the area immediately back of the Arctic Research Laboratory. The ground was still largely covered with snow, but a number of Lapland Longspurs (*Calcarius lapponicus*) and Snow Buntings (*Plectrophenax nivalis*) already had territories in the area between the laboratory and the dump. At first Green was reluctant to fly, because of the wind of about 20 miles per hour from the north. Finally, she flew at a pair of longspurs, just as they left the ground about 20 yards away. She stayed with them for about 75 yards but did not try to close, finally veering off to land atop a pole. The longspurs then towered up above the perched shrike, uttering alarm calls. They attracted the attention of six to eight Snow Buntings—mostly males—and these came flitting up, also giving alarm cries. They flittered around above the shrike off and on for 15 minutes. Several times the shrike made a brief dash at one of the buntings yet never seemed determined in pursuit. After a time, the buntings stopped their persistent pestering of the shrike and resumed territorial interactions and displays; but whenever the shrike made an obvious move on its perch or flew a short distance to a new perch, all the buntings reassembled, flitting about above the shrike. It was curious to see how these territorial males, which a moment before had been chasing each other, assembled so quickly into a flock to mob the shrike. Several times during a mobbing episode, two male buntings suddenly broke off and attacked each other in the air, even binding together with their feet.

The shrike sat out for about 30 minutes. Then she suddenly became interested in something on the ground about 30 yards away among some old oil cans supporting a pipeline. The shrike swooped off her perch and dropped down onto one of the cans. A small brown lemming (*Lemmus trimucronatus*) was foraging at the base of the can, where the snow had melted away. The shrike jumped down by the rodent, but the lemming did not attempt to flee; and the shrike simply grabbed it by the neck with its beak in the usual manner. I moved in slowly and set the cage down three feet from the shrike. As soon as the lemming stopped kicking, the shrike picked it up in her beak, flew into the cage with it, and impaled it on a piece of sharp wire. The lemming was a juvenile male weighing 15 grams.

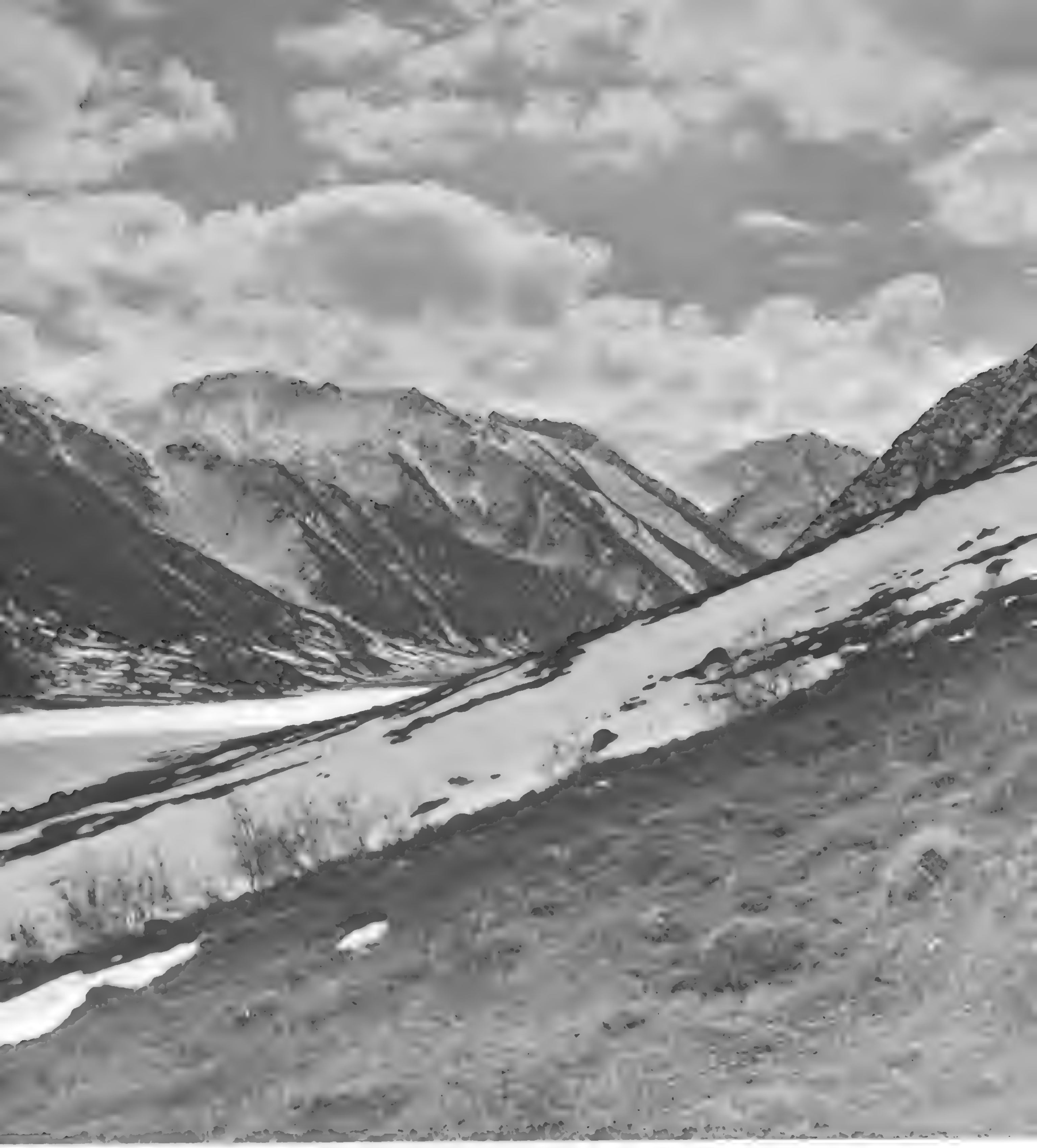

Figure 5. Willow brush habitat of the Northern Shrike around Lake Peters. Note the thin line of willows outlined against the snowbank just north of Area 9. Chamberlin Glacier appears in the upper left background.

17 June 1961, 2:45 to 3:45 PM, Lake Peters, Alaska.—I took Green out in a strong wind of about 20 mph. The sky was clear to partly cloudy. We got no flights at birds, but Green caught 45 assorted flies and other small insects, most of which were grounded by the wind. She did spot one bumblebee (*Bombus* sp.) flying over the lake about 100 yards away and neatly snapped it out of the air with her beak.

22 June 1961, 1:00 PM, Lake Peters.—Carrying Green in the portable cage, I walked up to within five yards of a male longspur, perched atop a large rock on one of the alluvial fans, and opened the cage door. At first the shrike did not show any inclination to chase (she had previously been reluctant to chase male longspurs, which she could seldom catch). Then, the longspur jumped off the rock to forage on the back side, out of view of the shrike. Green immediately dropped out of the cage and, concealed by the rock, flew low over the ground until she came up over the top and pounced on the longspur. The prey eluded the strike, though very narrowly, and flew off downhill. The shrike did not follow.

23 June 1961, 6:00 PM, Lake Peters.—While walking along a ridge back of camp carrying Green in her cage, a fledgling Horned Lark (*Eremophila alpestris*) flew up about 10 yards away. The shrike gave immediate pursuit and struck at the lark in the air after a short chase. I do not know whether she hit the lark, but it went down on to the ground at once. Green turned back on it, bound with her feet, and bit into its neck twice—all in very quick succession. At the same moment, a mob of small birds converged around the shrike—the two parent larks, eight to ten Lapland Longspurs, mostly males, and a pair of Baird's Sandpipers (*Erolia bairdii*). The shrike sat upright by the dead lark, watching the other birds. They flitted all about in the air, sometimes landing briefly on the ground near the shrike and then flying up again. The parent larks showed less agitation and persistence than the longspurs, which came in very close to the shrike, uttering their constantly repeated *cheer* or *dear* alarm notes. Finally, the shrike started trying to carry the lark away. At first she made several attempts to fly up with it in her beak but could not stay airborne. After the third or so try, she made a jump to take off with the lark still in her beak and then quickly transferred it to her feet, managing thus to fly off downhill, gaining altitude. She flew about 200 yards away and landed under a tracked vehicle, where she stayed until I came up.

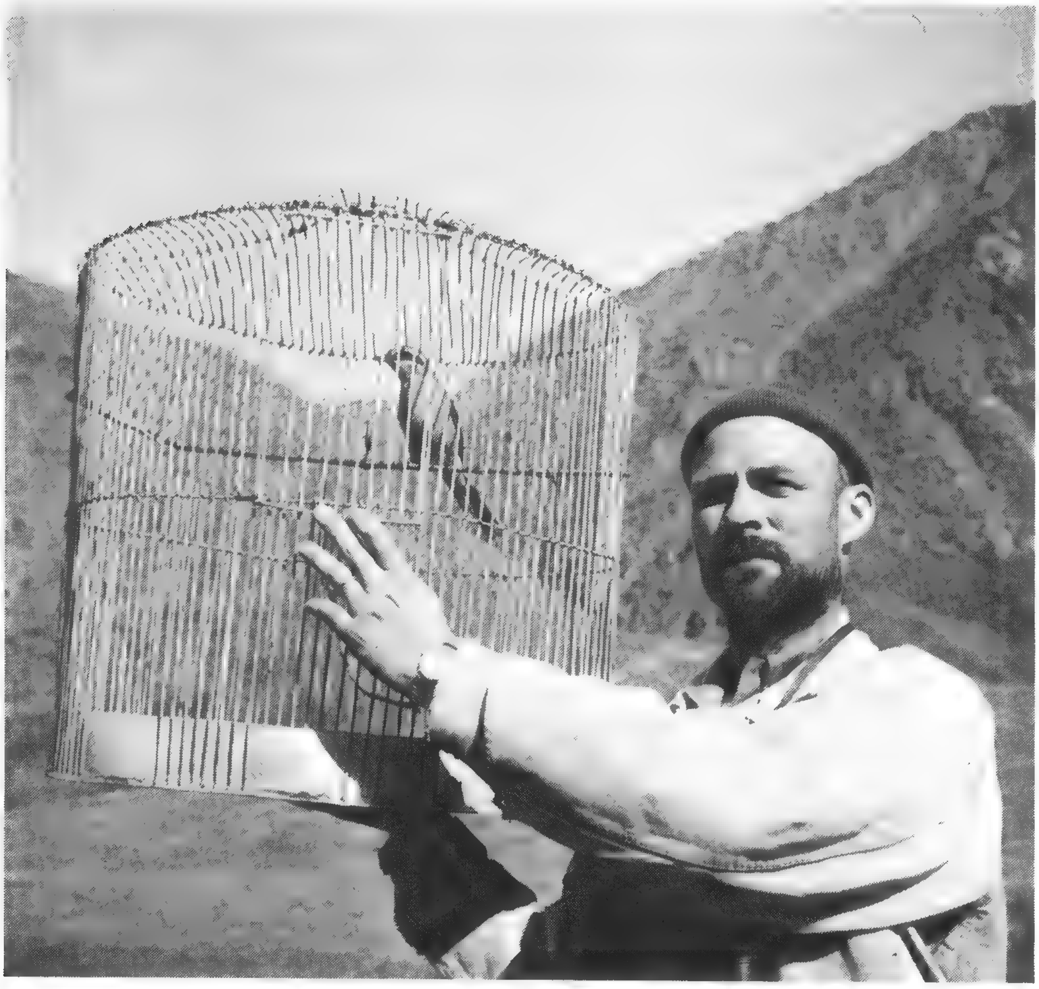

Figure 6. A trained shrike, "Green," about to be released from her carrying cage to hunt on the camp fan, Lake Peters, June 1960. Photo by John Hobbie.

27 June 1961, 12:00 to 8:00 PM, Lake Peters.—Green flew free around camp all afternoon. She caught many bumblebees on the wing, and I found a decapitated fledgling longspur, which she apparently killed when I was not watching. Again, I was impressed by how she bided her time and waited for the best advantage. On one occasion, she sat on top of a big rock high up on the alluvial fan. Many small birds—larks, Water Pipits (*Anthus spinoletta*), redpolls (*Acanthis* sp.), longspurs, and buntings—were excited by her presence and kept flitting about and calling 15 to 20 yards away from the rock. When they flew by fast close to the rock, the shrike showed not the least inclination to chase; but this was not the case with a Water Pipit that came flitting straight toward the rock, headed up into the wind, so that it was slowed down. When it was about 10 yards from the rock and still headed straight for it, the shrike suddenly attacked, and there was a long, down-wind chase of several hundred yards. The pipit finally escaped by ringing up over the lake and out-climbing the shrike. As the shrike turned away from the pipit, she caught sight of a bumblebee flying fully 100 feet up in the air and snatched it in her beak while executing a beautiful swooping pass.

23 September 1962, 5:30 PM, Manlius, New York.—"Predaceous," a 75-gram juvenile male, was flown on rolling pasture land with hedges and trees along old fence rows. The shrike first attacked an Eastern Kingbird (*Tyrannus tyrannus*) and drove it away. Then there was a long encounter lasting about 30 minutes with a flock of American Goldfinches (*Spinus tristis*). These birds took refuge in two willow trees. I kept flushing them back and forth between the trees for the shrike. At first he pursued very eagerly, and once in a long, open flight he nearly caught a bird. It was obvious that he was trying to snap at the finch with his beak in the air rather than grabbing it in his feet. Gradually after several failures he began to lose interest in the goldfinches, and finally, even when I brought him within four feet of one perched in a thistle, he refused to chase it.

27 October 1962, 4:00 PM, Manlius.—As I walked out into a field of high, dead grass, a Savannah Sparrow (*Passerculus sandwichensis*) flushed almost under my feet. The shrike, Predaceous, banged against the inside of the cage before I could let him out. I opened the door, and the shrike went out after the sparrow, now about 40 yards away. On seeing the shrike, the sparrow quickly dropped back into the grass. I rushed in as the shrike flew off and higher. I called to the shrike, and he turned back toward me just as I flushed the sparrow. The shrike came down hard and fast, but the sparrow put into the grass again—this time very close to me. I flushed it again, and the shrike was right on top of it as it tried to go into cover. Sparrow and shrike both disappeared into the grass, and I soon heard the sparrow giving distress calls. Another Savannah Sparrow then flew over the field and hovered above the shrike, pointing out his location until I walked up. I held the cage down by the shrike, and he carried the sparrow right in, even though he was scolding me and was fluffed out in an aggressive posture.

28 October 1962, 9:45 AM, Manlius.—I released the shrike in the same area mentioned above. There was a strong wind blowing. Instead of following me closely, the shrike made large sweeps up to one-quarter of a mile back and forth along the fence rows, often 200 to 300 feet up in the air. Occasionally, he came down and hovered over me in the field. Then a flock of six to eight small birds flew over at about 500 feet. The shrike chased after them over a wide radius of about one-quarter of a mile, never able to catch up or gain equal altitude. Finally the flock flew over me with the shrike trailing behind.

I called to the shrike, and he began to come down. When he was about 100 yards away, I released a domesticated Canary (*Serinus canaria*). The Canary flew up and circled back, heading toward the shrike. The shrike swooped down and tried to force the Canary to ground. The Canary flew toward a row of trees. The shrike swooped back and forth over the Canary several times. Just before the Canary reached the trees, the shrike finally grabbed it in his feet and fluttered down to the base of some trees with the prey. As I walked up, the shrike was still killing his quarry on the ground. I tried to work through some brush to place the cage down for the shrike. The shrike was skittish and moved under a fence. I tried to go to the other side. In the meantime, the shrike flew off with the Canary. I did not see where and lost all contact with the shrike for 30 minutes. Later, as I was walking along a fence row some 200 yards from the site of the kill, the shrike suddenly flew to me from an undetermined quarter. I called him into the cage. He had Canary feathers adhering to his beak.

Generalizations

From these and many similar observations, some of which have been published elsewhere (Thielcke, 1956; Cade, 1962; Mester, 1965), one can build a general description of the hunting tactics used by the Northern Shrike. The Northern Shrike has two methods of hunting. One is to perch on some high vantage, usually the upper branches of a tree or bush and keep a careful watch for quarry moving on the ground or in the air below. When the shrike chooses its prey, it shoots straight down and flies just over the surface of the ground, often using concealing objects to remain hidden from the quarry's view. Thus, like an accipiter, the shrike frequently appears to catch its prey by surprise.

The shrike's second method of hunting is to move about actively on the ground, through bushes, or among the branches of trees in apparent attempts to flush quarry into flight. In this method the shrike often employs special wing movements (see Zimmerman, 1955; and Cade, 1962, for details). It is more likely to use this method after it has failed to make a capture by the first method, and the prey has escaped into dense cover. Sometimes the shrike also hovers briefly over a spot where it has seen prey moving and will attack from such a position if an opportunity arises.

The Northern Shrike often pursues small birds in flight, occasionally catching one; but I believe aerial capture is rare and that birds are most often taken by surprise while perched on the ground or in bushes and trees (see also Mester, 1965). A small bird, hard pressed by a shrike, always seeks the protection of dense cover—grass, brush, or thickly branched trees—in which it "freezes" and from which it leaves only under great duress. Rather frequently, however, the frozen bird is taken by surprise and captured before it moves from its branch.

The Northern Shrike usually catches birds in its feet, although a few times I have seen both wild and trained shrikes attempt to strike down a flying bird with their beaks, and White (1963) describes a hunt in which a wild Northern Shrike appeared to strike a Pine Grosbeak (*Pinicola enucleator*) with its beak before grabbing it in its feet. On the other hand, a shrike does not grab a rodent in its feet, because it is likely to be bitten. Instead, it harasses the rodent by jumping and "dancing" erratically around the prey, reaching in when the advantage is right to deliver a series of quick bites (see also Thielcke, 1956). Either on the ground or in flight, the shrike always snaps up insects in its beak.

The vision of the Northern Shrike is extremely acute, perhaps sharper even than that of most hawks. According to Thielcke (1956), in Germany a butcherbird sitting on a high perch can see a mouse running on the ground at a distance of 80 meters (approximately 100 yards) and will fly to attack another shrike at a distance of at least 450 meters (about 560 yards). My observations indicate that Thielcke's estimates are conservative. In the wintertime around Syracuse, New York, I have had wild shrikes fly directly from their tree-top perches to a trap baited with a mouse or small bird over courses in excess of 200 yards, and I have had wild shrikes fly to attack caged shrikes or free-flying trained birds from distances approaching 1,000 yards. Green could spot flying bumblebees at least 100 yards away, a distance at which they were quite invisible to my eyes, although I could easily pick them up in 7 X 50 binoculars once the shrike had shown me their position. Some movement of the prey is, of course, essential for any of these responses.

I should emphasize one final point about the hunting habits of the Northern Shrike. This species, a persistent hunter and tracker, has a highly developed ability to return to the specific locations where it has seen prey go to cover. Here are examples. One winter around Syracuse, I saw a Northern Shrike chase a meadow vole (*Microtus pennsylvanicus*) over open ground and make a determined strike at the vole just as it disappeared down a hole. The shrike sat peering at the hole for several seconds and then flew into a nearby bush about three feet off the ground where it sat watching the hole for 30 minutes and was still watching when I departed. Once at Lake Peters in 1960, a pair of White-crowned Sparrows (*Zonotrichia leucophrys*) built a nest on the ground at the base of some willows about 100 yards from a shrike nest. After the female laid eggs, and incubation was under way, the male shrike noticed the activity to and from this nest and returned repeatedly to perch in the willows nearby. I saw him chase these sparrows several times. Although I did not see him actually catch one, I have strong circumstantial evidence that he did. A few days later I found an adult female White-crowned Sparrow with a brood patch impaled in the shrike's larder, and the sparrow nest abandoned. Finally, I used to exercise one of my trained shrikes in the basement of my home. At one time I also had a melanistic pocket mouse (*Perognathus flavus*), which I kept in a transparent plastic box on a work table in the basement. Ordinarily I covered the box with a cloth before flying the shrike loose, but once I forgot, and the shrike immediately saw the mouse and attacked it in a most violent manner, trying to find a way into the box. After I covered over the box with the cloth, the shrike repeatedly returned to the table and looked about the covering, as though expecting to find the mouse. The same kind of investigative behavior was repeated regularly each day for more than a week; and even a month later the shrike still occasionally inspected the cloth covering the box, although he never again saw the pocket mouse. In the wild, persistent watching at a mouse hole or bird nest should be a profitable way for a shrike to collect prey.

The Killing Mechanism

Review of Old Ideas

How does the Northern Shrike kill its prey? One reads many conflicting and anthropocentric statements about how shrikes kill and "torture" their prey. One of the commonest misconceptions is that the shrike impales live quarry and leaves the hapless victim struggling until it finally dies. It may be that insects are sometimes spiked before all their reflexes are lost, but I have never seen a shrike impale any vertebrate quarry before it was dead, nor have I read of an authenticated instance.

The Nunamuit Eskimo living in Anaktuvuk Pass call the shrike "Irirgik," meaning "eye extractor." This refers to their belief that the shrike picks out the eyes of small birds and mice, and then watches the blinded victim blunder about until ready to eat it (Irving, 1960). The same name and story were current among the Kobuk people when Grinnell (1900) worked in the Kotzebue Sound region. This belief may originate from the fact that the Northern Shrike begins eating impaled birds and mice from the head down, gradually working posteriorly. The orbital region is one of the easiest places for a shrike to tear into the head, and it often happens to eat the eyes first.

Other ideas, included in the life history accounts of Bent (1950), are that the shrike kills by penetrating the brain of its prey with its beak or that it kills by harassing, shaking, and pounding the quarry until it dies of exhaustion and generalized injuries. Bent correctly points out, however, that the usual way of killing is by biting into the neck of the quarry.

Inferences from Wounds on Freshly Killed Prey

Since the hooked beak and the powerful jaw muscles are the only features of a shrike's anatomy that are obviously modified for predatory actions, one would expect *a priori* that its method of killing involves these structures. Unfortunately, when one observes a wild shrike in the act of pursuit and capture, it is usually difficult to see exactly what takes place; but if he can secure the carcass of the prey immediately, he can draw certain inferences from the nature of the wounds.

Table 1 summarizes information about the way shrikes treat their prey. Of primary interest at the moment is the fact that the lethal wounds made by shrikes show a striking degree of uniformity from one prey carcass to the next. In only one case, in which it was possible to determine clearly the cause of death, was there any wound other than on the neck. Also, in contrast to the lack of external signs of damage on the carcass—often the skin was not even punctured—the amount of internal injury to the neck was impressive, the cervical vertebrae often being severed in two or three places with extensive hemorrhaging and mangling of the muscles and soft tissues from the shoulders to the base of the skull. This kind of wound at once reminded me of the stereotyped manner in which falcons kill their prey—that is, by a series of sharp bites which sever the cervical vertebrae. Subsequent observations on wild and tame shrikes proved that the attack is always immediately directed at the neck of the quarry, and in no case have I seen any other method of killing employed than by a series of grabs and bites at the neck. Miller (1931) reached the same conclusion for *Lanius ludovicianus,* the Loggerhead Shrike.

This conclusion refers specifically to vertebrate quarry. Shrikes snap up insects in their beaks and crush thoroughly the larger ones, such as grasshoppers and bumblebees, by repeated bites, mainly in the region of the thorax, as they manipulate the insects in their beaks.

Structure of the Beak

Figure 7 calls attention to the noteworthy fact that both falcons and shrikes possess conspicuous tooth-like projections on each side of the maxillary tomium (the cutting edge of the maxilla or upper beak) just posterior to the hooked tip. For some time I have been intrigued by the idea that the tomial "teeth" of the falcons play some part in the mechanism of their killing

TABLE 1

Treatment of Avian and Mammalian Prey by Northern Shrikes in Arctic Alaska

Height prey is hung		*Method of hanging*		*Major wounds*	
Feet	*Number cases*	*Description*	*Number cases*	*Description*	*Number cases*
0-1	3	Spiked through scruff of neck	16	Cervical vertebrae severed near base of skull	12
1-2	7	Spiked on back under shoulder	5	Cervical vertebrae severed in midregion of neck	55
2-3	10	Spiked under armpit	3	Thoracic vertebrae severed	1
3-4	19	Spiked through back of skull	2	Animals showing no external marks of injury	44
4-5	20	Hung by neck and head through fork of branch	18	Wounds obscured by impaling or feeding	26
5-6	22	Hung by shoulders and forelegs through fork	17		
6-7	12	Hung by throat on snub	4		
7-8	5	Laced through terminal spray of twigs	7		
8-9	7	Lying on belly through fork of branch (mammals only)	6		
9-10	4	Neck twisted about snub on branch (birds only)	3		
10-11	3	Unclassifiable ways	23		
11-12	2				
Totals	114		104		94

response (Cade, 1960), and now, in the case of the shrikes, we can see the same association between a structure and a piece of behavior. What we seem to have is a remarkable instance of a highly specific kind of structure, which is used for an equally specific kind of action, independently evolved in two quite distinct groups of predatory birds.

The structural aspect of the adaptation seems to be somewhat more highly evolved and older in the falcons, for their teeth are represented by bony substructures on the maxilla itself, as well as by the horny projections of the tomium, and the mandible (the lower beak) possesses notches into which the teeth fit. The teeth of the shrikes consist only of horny projections of the tomium, and there are no mandibular notches, although the contour of the mandibular tomium is scalloped into a concavity in the areas that come into apposition with the maxillary teeth.

Experiments on the Function of the Tomial Teeth

My first hypothesis was that the teeth serve as wedges to which the full force of the bite can be applied, sinking the teeth into the soft tissues of the neck and in between the vertebrae to disarticulate them. To test this hypothesis I did the following experiment with an adult female shrike weighing 70 grams. She was allowed to kill a series of 10 adult male laboratory mice weighing 25 to 30 grams. Two variables were measured: First, the time elapsing between the initial grab at the neck and the point at which the mouse was immobilized, and second, the number of grabs at the neck required to kill the mouse. Then I cut off the tomial teeth of this same shrike and filed the surfaces of the tomium to a smooth contour. After a rest of 24 hours, the shrike was allowed to kill 10 more mice. My reasoning was that if the tomial teeth play an important role in the killing, then there should be a significant difference between the two sets of measurements.

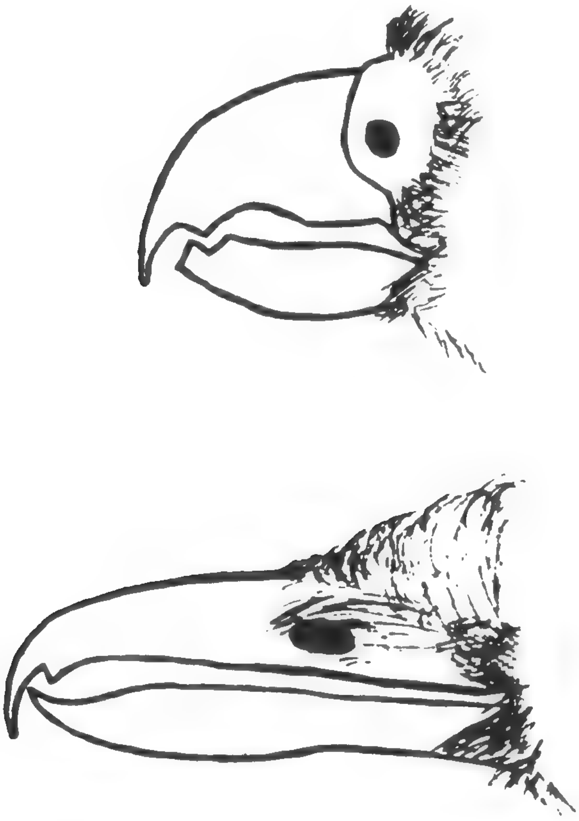

Figure 7. Comparison of beak shapes between a falcon (upper) and a shrike (lower). Note the similarity in shape and position of the tomial teeth.

Table 2 summarizes these data which, unfortunately, support no such easy conclusion. If anything, the performance improved in the series of tests without the teeth; but this improvement, if indeed real, can be attributed to the shrike's increasing familiarity with the limitations of her cage and with the escape tactics of laboratory mice. There do seem to be some subtle differences in the kind of wound made under the two sets of conditions. With the tomial teeth removed, the degree of hemorrhaging and mangling of the muscles around the neck was much increased, and in seven out of the 10 cases one or more of the severed vertebrae were crushed or broken. With the teeth present, the disarticulations were always clean, and there was breakage of bone in only one case.

I was undismayed by these results. After all, a laboratory mouse is not very difficult quarry for an adult Northern Shrike, and it might be that the teeth do not come into critical play until the shrike is attacking quarry near the maximum size possible for it to kill. So I did the experiment a second time using laboratory rats weighing 50 to 70 grams. Table 3 shows the results. Again there were no significant differences. It takes a shrike a much longer

TABLE 2

Influence of Tomial Tooth on the Ability of a Northern Shrike to Kill Laboratory Mice Weighing 25 to 30 Grams

Kills with tooth present			*Kills with tooth absent*		
Killing time in seconds	*Number bites*	*Type of wound*[1]	*Killing time in seconds*	*Number bites*	*Type of wound*[1]
32	5	A	7	1	A, E
6	2	B	10	1	G
10	3	A	9	2	A
27	4	A, D	9	3	A, B, E
15	7	A, E	4	1	A, E
26	5	A	11	5	B, C
28	8	A, B, F	4	3	A, E
33	6	A	30	6	A, E
20	5	A	6	2	C, E
14	5	A	18	4	A, E
Range 6-33	Range 2-7		Range 4-30	Range 1-6	
Mean 19.0	Mean 4.3		Mean 10.7	Mean 2.9	

[1] A — mid-cervical vertebrae, including nerve cord, cleanly severed.
B — second and third cervicals partly severed; nerve cord exposed.
C — mid-cervicals partly severed; cord exposed but not cut.
D — atlas (first cervical) partly severed from occiput; cord exposed.
E — vertebrae crushed or broken.
F — thoracic vertebrae partly severed; cord exposed but not cut.
G — atlas and axis (second cervical) partly severed; cord exposed but not cut.

time and many more bites to kill rats by comparison with its quick dispatching of a mouse, but the absence of the teeth made no difference in the time or the number of grabs. There were two cases of broken vertebral processes with the teeth absent, none with the teeth present.

Such data might well be embarrassing, if not downright discouraging, to a person of less firm conviction, but I still believe the tomial teeth have been selected in these species as structural parts of their mechanism for killing prey. The occurrence of tomial teeth in association with biting to disarticulate cervical vertebrae in two independently evolved groups of predators is too compelling to allow one to place much confidence in the outcome of these experiments.

Two suggestive facts do emerge from these experiments. First, the wounds made with the teeth intact appear to be neater with a minimum breakage of bone. Second, in no case was the shrike able to sever completely the cervical vertebrae of a rat. In most cases the cervicals in question were sprung apart, and the nerve cord was exposed between the vertebrae but not severed. Now, the rats always lost control of their locomotor coordination some time before they were finally killed by the shrike—as though some tracts in the cord responsible for locomotion were injured early in the attack.

I suspect that the teeth serve as devices for penetrating quickly to the cord through the space between the articulating vertebrae to damage the cord and to produce partial paralysis, thereby rendering the quarry easier to kill. In the confinement of its cage a persistent shrike will, of course, manage to kill its quarry with or without the teeth; but in the wild there are frequent opportunities for the quarry to escape, so that every bite delivered to the neck should be as effective as possible. In nature, then, there should be a selective advantage for a device that renders the quarry less mobile. I venture the suggestion that the major adaptive advantage of teeth, both for falcons and for shrikes, is that they enable these birds to kill larger prey than would be possible without the teeth and that the kinds of prey available to these species are thus greatly increased. At any rate, the subject merits more study.

The tomial teeth may also be used for feeding. Since both falcons and shrikes typically break up long bones into short fragments before swallowing them, the teeth might be used for this purpose. A shrike will often tear off an

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TABLE 3

Influence of Tomial Tooth on the Ability of a Northern Shrike to Kill Laboratory Rats

Kills with tooth present				*Kills with tooth absent*			
Weight of rat	*Killing time in seconds*	*Number bites*	*Type of wound*[1]	*Weight of rat*	*Killing time in seconds*	*Number bites*	*Type of wound*[1]
71	420	70	A, E, F	72	127	98	A
69	127	61	A, D	67	290	117	A
69	190	38	E, F	66	45	25	A
66	327	71	A, D	63	175	35	A
65	140	31	E, F	61	170	51	A, B, D
58	233	67	A, C	60	140	27	A
57	185	23	A	60	120	24	A
57	45	20	A, D	56	63	18	A, C
54	55	26	A	54	220	30	A, B
53	50	21	A	53	111	31	A
Range 53-71	Range 45-420	Range 21-71		Range 53-72	Range 45-290	Range 18-117	
Mean 61.9	Mean 177.2	Mean 42.8		Mean 61.2	Mean 146.1	Mean 45.6	

[1] A — atlas and axis separated at dorsal contacts; nerve cord exposed but not severed.
B — neural arches of axis crushed.
C — articulating processes of axis and third cervical separated but cord not exposed.
D — atlas partly separated from occiput at dorsal contact but cord not exposed.
E — atlas nearly severed from occiput and cord exposed.
F — atlas and axis slightly parted; cord not exposed.

entire forelimb from a mouse carcass, and then work the member back and forth in its mandibles, carefully snapping all the bones before swallowing the leg whole.

Impaling and Feeding

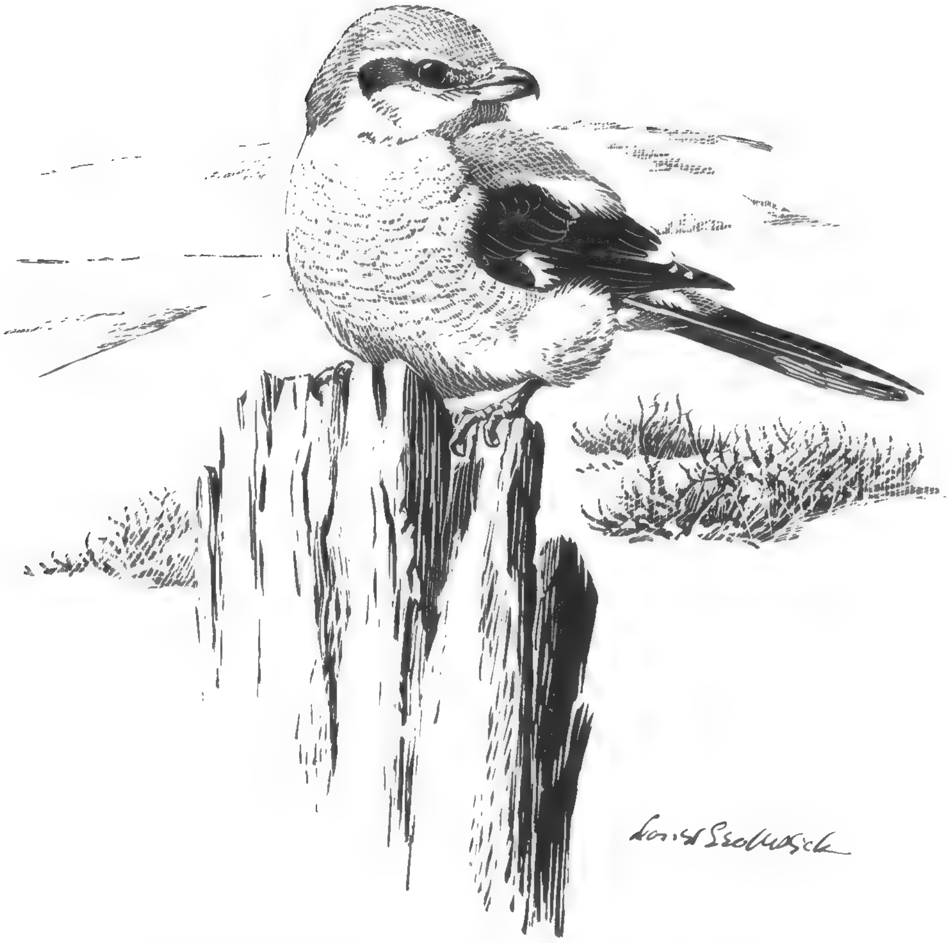
Once it has killed a large animal, the Northern Shrike manifests a strong urge to impale the quarry on a suitable spike or to hang it up in the fork of a branch. Small insects are snapped up and eaten in one process; larger insects may be held in the foot and eaten, as a kestrel eats a grasshopper, or spiked on a thorn to be dismembered at leisure; but all vertebrates are first impaled or hung in a branch before they are eaten.

The shrike carries insects and small vertebrates, weighing less than about 20 grams, from the point of capture to the impaling site in its beak. It picks up larger quarry, weighing more than about 20 to 25 grams, in its beak and then, just as it launches into the air, transfers the quarry to its feet. In its feet the shrike carries the quarry posteriorly under the tail, as a hawk does. Apparently large quarry, carried in the beak, makes the shrike nose-heavy and aerodynamically unstable, so that when the prey weighs roughly one-half the weight of the shrike, the bird must transfer it to a posterior position. Once airborne, especially with a downhill start, the Northern Shrike can carry remarkably heavy quarry—fully adult voles and lemmings, adult robins and larks—species about comparable in weight to itself.

The shrike usually lands with its quarry in the lower branches of the impaling tree or bush and then works its way up to a suitable position by hopping from branch to branch. It then proceeds in what looks like a more or less random, trial-and-error fashion to try out various possible impaling devices. The quarry is worked into a potentially suitable position, and then the shrike pulls on the quarry in attempts to spike it or wedge it firmly into place. It may try many times before the quarry is finally secured, and the impaling behavior seems to be "turned off" only when the quarry remains fast in position as the shrike tugs at it. If hungry, the shrike will dismember the quarry and feed at once, beginning with the head and working posteriorly. Otherwise, it may sit quietly by the impaled carcass for a few minutes, and then fly off to hunt again.

During the breeding season the shrike often—but by no means always—maintains larders in the nesting area. I have found as many as 12 vertebrate carcasses hung up at one time in a larder at Lake Peters. The booty is not near the nest — the closest items I found were about 50 yards away, the farthest over 200 yards. If one takes a carcass and hangs it closer than about 50 yards from the nest, the adult shrikes quickly remove it to a position farther away. Since the larder sometimes attracts foxes and other mammalian predators, it is therefore advantageous for the shrike to keep the food some distance from its nest.

One sometimes sees stated that shrikes are insatiable killers, taking prey far in excess of their needs, and that many of the items impaled in the larders go to waste. This has not been the case with larders I found around nests in arctic Alaska. With few exceptions, the kills were used. Now and then an individual carcass might have hung for a week or more, but eventually it was eaten. Shrikes, with their excellent sense of location, do not forget where they place their quarry. Occasionally a carcass may dry out before it is eaten or, in winter, may freeze solid. Then the shrike probably abandons it, but such



Northern Shrike. Drawing by Donald Leo Malick

instances are rather the exception than the rule in arctic Alaska. Miller (1931) gave a rather different picture for the Loggerhead Shrike in California.

Table 1 presents information about birds and mammals found in the larders of shrikes nesting in arctic Alaska, mostly around Lake Peters. The shrikes hung their prey at any height from ground level to about 12 feet up, with the great majority of items from three to seven feet up. In one case a longspur, found wedged into the forks of a decumbent willow, was lying on the ground. In this region, where there are no thorny trees or shrubs and no barbed-wire fences, the jagged tips of broken twigs and branchlets provide the only spikes for impaling. The shrikes use a variety of methods to secure their quarry in addition to impaling in the strict sense. About 25 per cent of the cases reported in Table 1 involved some manner of spiking or impaling, while more than 46 per cent of the cases involved the use of a forked branch, reflecting the much greater availability of suitable forks than spikes.

The Prey of Shrikes

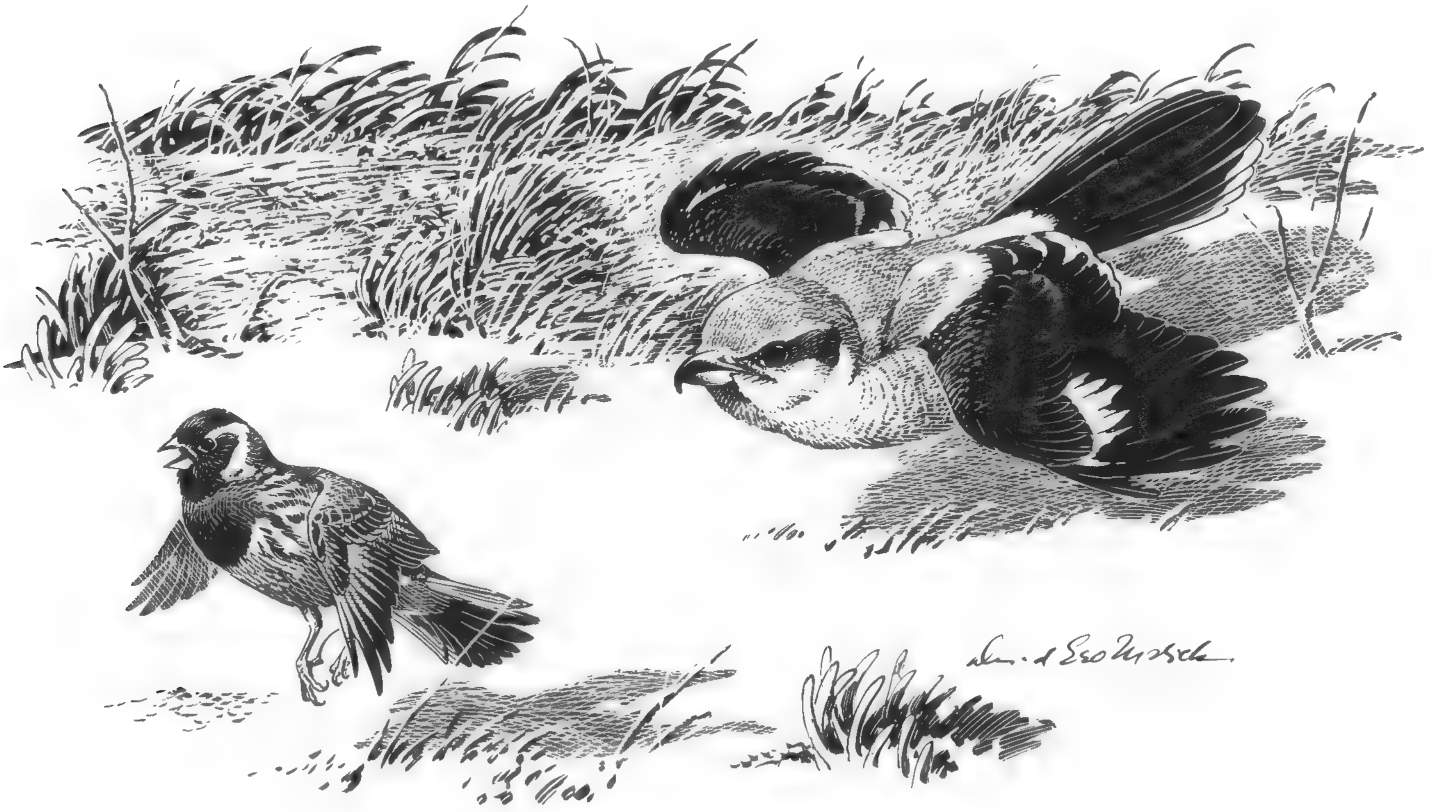
Methods of Study

A basic question one asks about any predator is: What kinds of animals does it eat? One may use a number of methods to get this information. The most obvious way—direct observations of the predator in the act of killing or eating its prey—can be quite profitable for some kinds of relatively sedentary predators, but for active avian hunters direct observations are difficult and opportunities for making them are infrequent. In the breeding season when the nest becomes the center of a great deal of feeding activity, one can obtain valuable data by observing from a blind, or by automatic recording with a camera, the kinds of food brought to the young.

Probably the method used most frequently in the past has been to collect samples of dead specimens and analyze the contents of their stomachs. The old Bureau of Biological Survey—forerunner of the Fish and Wildlife Service—obtained a vast amount of information this way in its attempt to establish the so-called "economic value" of many kinds of North American birds and mammals.

Fortunately for the birds of prey, there is one other very good method, a technique based on a peculiar feature of the alimentation of these birds. Many predatory types of birds ingest large quantities of indigestible materials along with the flesh they eat—bones and pieces of skin with hair or feathers attached. This indigestible matter is formed into a somewhat cylindrical, compact pellet in the stomach, and at intervals this pellet is regurgitated from the crop. Such pellets accumulate in or below the nest during the breeding season and at favored roosting places at all seasons. With practice and a good reference collection of specimens it is possible to identify to genus or species most of the fragments thrown up in these pellets, or castings as they are called in the falconer's terminology. They therefore provide a useful means for determining the foods eaten at all seasons of the year. All hawks and owls form such pellets, as do many other kinds of predaceous birds—various gulls, jaegers, herons, ravens, and shrikes. In addition, the shrikes' larders, often near their hunting areas or near their nests, provide an easy way to survey their prey.

An examination of pellets can reveal not only the kinds of prey eaten, but also—with some limitations—the relative numbers of the different species taken. Estimating the numbers of individual prey animals represented by a sample of pellets depends upon counting some single, easily identified part



Loggerhead Shrike in pursuit of a male Lapland Longspur. Drawing by Donald Leo Malick.

of an organism, and the accuracy of the estimate depends upon how consistently that part is eaten by shrikes. For example, a shrike usually discards the hindlegs of a grasshopper and frequently, too, the feet and tarsi of birds. Counting these parts in a collection of pellets would lead to a gross underestimate of the numbers of grasshoppers and birds represented. On the other hand, the shrike nearly always swallows the heads of grasshoppers, usually intact; and one of the identifiable parts of a bird that it most frequently swallows is the proximal end of the humerus.

I based my determinations of numbers of prey in pellets on identification and counts of the following parts: for birds, the humerus; for mammals, the lower jaw; for bumblebees, wasps, and some other insects, the head; and for beetles, the elytron (the thickened forewing that covers and protects the hindwing). I judge that mammalian jaws are the most reliable of these indices of numbers, bee and wasp heads are next, bird humeri are a poor third, and the beetle elytra are so often fragmented in the pellets that counting the intact ones is probably fruitless. Thus, my estimates of numbers are most accurate for mammals, large insects, and birds, in that order; but my estimates of the numbers of small insects are much too low. In all cases, the estimates represent minimum numbers of prey in the pellets.

Previous Findings

Most of the previously published information about the food habits of the Northern Shrike comes from studies of stomach contents of birds taken on their wintering grounds. In a sample of 67 stomachs collected between October and April in the United States, Judd (1898) found the remains of 28 small birds, including Tree Sparrows (*Spizella arborea*), juncos (*Junco* spp.), and House Sparrows. Mice were present in one-third of the stomachs, and insects occurred in some stomachs during every month of the winter, indicating that the sample must have come from the extreme southern perimeter of the winter range, or possibly that some stomachs of the Loggerhead Shrike were misidentified and mixed into the sample. Stegman (1959) analyzed an additional 140 stomachs obtained from the old collections of the Fish and Wildlife Service. Again, small birds, mice, and insects were the principal items found.

Except for brief references in faunal reports, the analysis of 23 pellets, reported by Murie (1946), from a nest of the Northern Shrike in Mount McKinley Park, Alaska, is all that has been recorded about food habits of the species on its northern breeding range in North America. Although Murie frequently saw shrikes chasing small birds and described some interesting accounts of these chases, the pellets he analyzed all contained the remains of microtine rodents; one also included a beetle, and another, a wasp.

According to the "Handbook of British Birds," the north Eurasian form feeds principally on small birds, secondarily on mice and insects; but Mester (1965) concluded that voles form the bulk of the food.

We have long known of the periodic winter emigrations of Northern Shrikes into the northeastern and north-central United States (Davis, 1937; 1949; 1960), and some researchers have implicated the species as one of the predators that fluctuates in numbers in response to the northern microtine population cycle. Figure 8 presents a re-graphing of Davis's data, based on information from the Audubon Christmas Bird Counts—with the addition of data for recent years, plus a comparison over the past 35 years with data from the western portion of the shrike's wintering range. Between the years

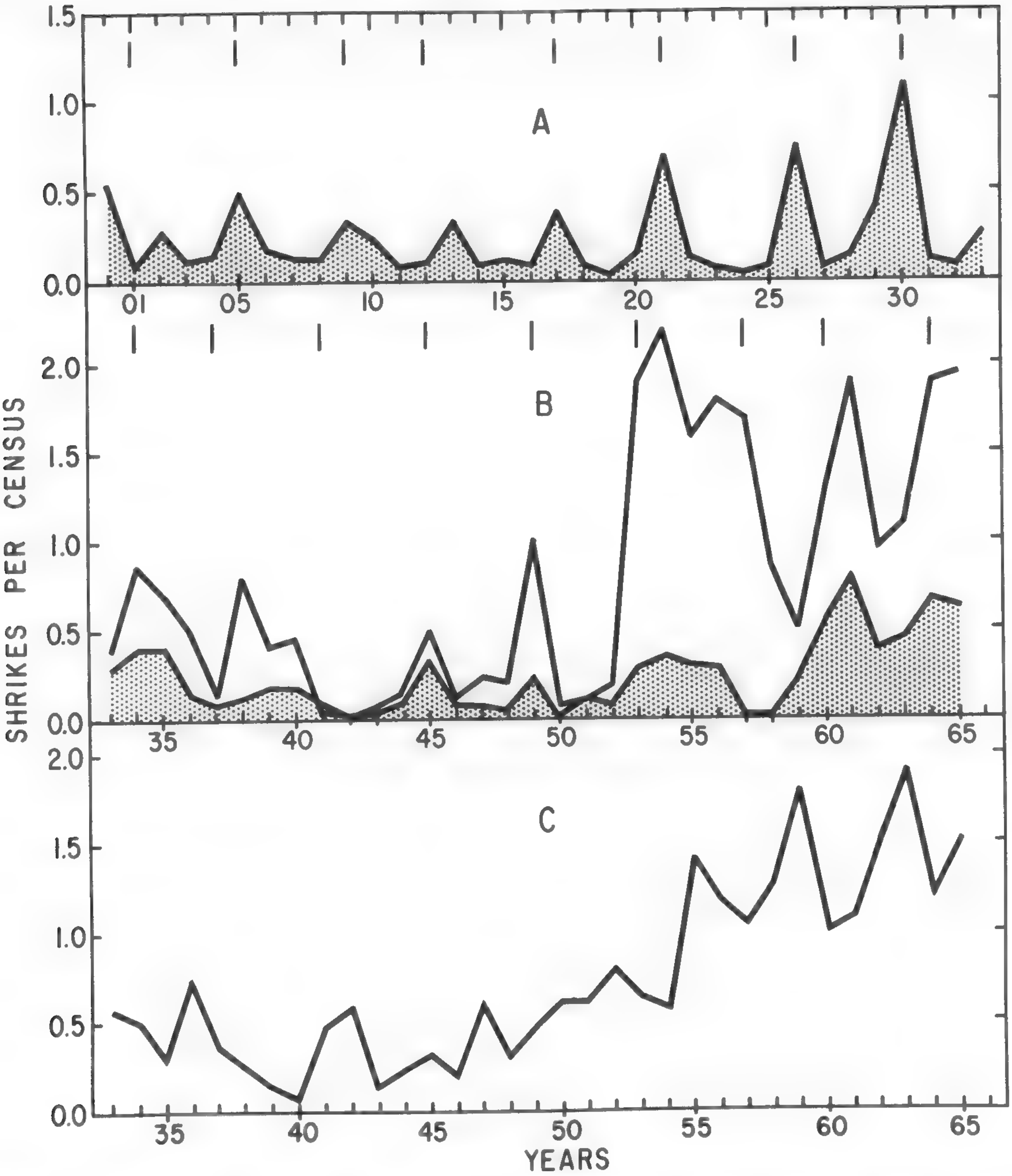


Figure 8. Numbers of shrikes reported on Christmas Bird Counts, 1900 to 1965. A. Northeastern United States and Great Lakes region (replotted from Davis, 1937). B. Same region as A, based in part on further analyses by Davis (1949; 1960) and in part on my own compilations from Christmas Counts published in *Audubon Field Notes, Audubon Magazine,* and *Bird-Lore.* The number of reports per year ranges from 50 to 298. The upper line, based on reports from Quebec, Ontario, and New York, represents findings within the "optimum" winter range; the number of counts equals 16 to 71 reports per year. C. Western range, including Alberta, British Columbia, North and South Dakota, Nebraska, Montana, Wyoming, Colorado, Idaho, Utah, Washington, and Oregon. The number of reports per year ranges from 16 to 87. Vertical lines in A and B indicate years of major Snowy Owl flights.

1900 and 1936 there was a fairly regular periodicity in the emigrations of shrikes into the northeastern and Great Lakes region of the United States, with intervals of about four years (range two to five). Densities seem to have been about five to 10 times greater during the peak years than during low years. For the most part, the peak years corresponded with the peak-year "invasions" of the Snowy Owl (*Nyctea scandiaca*), or deviated by one year at most. Moreover, these years of "invasion" also corresponded closely with the peak years in the fox fur returns analyzed by Elton (1942) from Labrador and Ungava. All this information does seem to support the idea that the shrike emigrations are tied in with the cyclic phenomena occurring in northern microtine rodent populations.

Curiously, during the last 30 years there has been much greater irregularity in the fluctuating numbers of shrikes seen during the Christmas Counts in the area covered by Davis's study and a less clear cut association with Snowy Owl invasions. His most recent conclusion is that the owls and shrikes "are not completely dependent upon the same food supply or other cause of emigration" (Davis, 1960). There is also some suggestion that the amplitude of the numerical fluctuations has decreased in recent years, while over-all numbers have increased, although one cannot be sure how much these changes may have resulted from changes in the relative number of censuses reported from poor shrike areas versus those reported from good shrike country (compare the two curves in the B part of Figure 8). The period from 1953 through 1965 is especially noteworthy, because shrikes have occurred in relatively large numbers during each of these winters in the east, except for 1957 and 1958. Clearly one needs detailed and quantitative information on the foods of the Northern Shrike from its breeding range before he can determine the full significance and explanation of these winter emigrations and changes in numbers.

Shrikes wintering in the western regions are rather completely out of phase in their numerical fluctuations with the eastern birds, and in general the density of the western birds seems to be higher than in the east but also on the increase, especially since 1950. Presumably these western shrikes are of the race *invictus,* which breeds in Canada westward from Hudson Bay into Alaska, whereas those emigrating into the more eastern states (Great Lakes region and the Northeast) are of the race *borealis* from Quebec, Labrador, and Ungava. I am uncertain whether there is any actual contact between these two breeding populations around the southern perimeter of James Bay; they may well be disjunct allopatric populations, although Moose Factory in northern Ontario is given as a breeding locality for *borealis* (AOU Check-list, 1957). It seems significant, however, that Manning (1952), who reviewed all pertinent literature and did considerable field work himself, found no evidence of shrikes breeding along the entire west coast of James Bay and southern coast of Hudson Bay from Moose Factory to York Factory, although the species is well known as a breeding bird around Churchill. Further, Todd (1963), after reviewing all the records for Moose Factory and other locales along James Bay, concluded that "there are no dependable reports of the species' presence in the region of James Bay, or anywhere south of the Hudsonian Life-Zone, in the breeding-season, nor should any such reports be expected."

Certainly the Alaskan shrikes are physically different birds from those that winter around Syracuse, New York, where the shrikes are presumably of the race *borealis.* The Alaskan birds are lighter in color, and adults seldom weigh less than 65 grams and often go to 80 grams; whereas, wintering birds around Syracuse are dark and seldom weigh more than 65 grams and may weigh as little as 50 grams. It seems likely that the two subspecies occupy somewhat different ecological niches in their respective breeding environments. It could be that *borealis* will prove to be more of a microtine specialist than *invictus,* or that there is a greater degree of regional synchrony in the microtine cycle over the range of *borealis* than obtains over the much larger range of *invictus.* Again, we need detailed information on actual feeding habits on the breeding grounds before confident statements can be made.

Data from Alaska

Table 4 shows the results from a sample of 109 pellets obtained at a shrike's nest in the Okpilak River Valley along the northern front of the

TABLE 4

Analysis of 109 Pellets from One Northern Shrike Nest on the Okpilak River, 1958

Species of prey	*Number pellets*	*Per cent frequency*	*Minimum individuals*	*Per cent total individuals*
Redpoll	1	0.92	1	0.57
Savannah Sparrow	1	0.92	1	0.57
Lapland Longspur	4	3.69	4	2.29
Snow Bunting	1	0.92	1	0.57
Unidentified bird remains	19	17.43	1	0.57
Total birds	25	22.94	7	4.00
Tundra vole, adults	1	0.92	1	0.57
Alaska vole, adults	27	24.77	20	11.43
Alaska vole, juveniles	31	28.44	23	13.14
Tundra redback vole, adults	2	1.84	2	1.14
Unidentified microtine remains	40	36.70	?	——
Total microtines	101	92.66	46	26.29
Bumblebees	49	44.95	50	28.57
Wasps	21	19.27	21	12.00
Carabid beetles	20	18.35	24	13.71
Other beetles	22	20.18	27	15.43
Other insects	12	11.01	?	——
Total			175	

Brooks Range in the vicinity of Mount Michelson, a few miles east of Lake Peters. First note the rather limited number of species making up the diet of this family—only four species of birds, three species of microtine rodents, and half a dozen kinds of insects. Microtine rodents—mainly the Alaska vole (*Microtus miurus*)—occurred in 93 per cent of the pellets and made up 26 per cent of the total estimated number of individual prey animals; songbirds occurred in only 23 per cent of the pellets and made up 4 per cent of the total number of prey. Bumblebees were the most common of the insects—as is the case in all the samples—occurring in 45 per cent of the pellets and constituting 28.5 per cent of the individuals. Other insects included wasps (*Vespa* sp.) and carabid beetles (*Carabus* spp.). This restricted list reflects in part the limited variety of the fauna in this region and in part the preference of the shrikes for certain sizes and kinds of prey.

Such data become more meaningful as one learns more about the habits of shrikes. For instance, one might suppose that the pellets found on the ground under a nest have accumulated there over the entire nesting period and represent a fair sample of the total food eaten during this time. A little simple arithmetic proves that this supposition cannot be true. Given an

TABLE 5

Analysis of 86 Pellets from One Northern Shrike Nest at Lake Peters, 1959

Species of prey	*Number pellets*	*Per cent frequency*	*Minimum individuals*	*Per cent total individuals*
Water Pipit	1	1.16	1	0.58
White-crowned Sparrow	1	1.16	1	0.58
Lapland Longspur	10	11.60	6	3.51
Snow Bunting	1	1.16	1	0.58
Unidentified bird remains	21	24.42	?	——
Total birds	34	39.53	9	5.26
Alaska vole, adults	13	15.12	13	7.60
Alaska vole, juveniles	9	10.37	8	4.69
Tundra redback vole, adults	8	9.30	6	3.51
Tundra redback vole, juveniles	6	6.98	6	3.51
Unidentified microtine remains	30	34.88	?	——
Total microtines	66	76.74	33	19.30
Tundra shrew (*Sorex tundrensis*)	1	1.16	1	0.58
Bumblebees	51	59.30	70	40.94
Wasps	20	23.26	22	12.87
Carabid beetles	21	24.42	21	12.28
Other beetles	13	15.12	15	8.77
Other insects	4	4.65	?	——
Total			171	

average brood of seven young and an average of two or three pellets per young per day, it is at once apparent that a sample of 109 pellets can represent only five to seven days of accumulation. Put in another way, seven young in 20 days of nestling life can be expected to produce around 400 pellets.

Now, this sample of 109 is the largest I have found under any nest. Many nests have only a dozen or so pellets. Observations from blinds set up near active nests reveal that the adult shrikes remove the pellets from the nest and deposit them some distance away, just as they do with fecal sacs, and it is only during the last days of nestling life and the first few days of the fledgling period, when both adults spend long periods away from the nest, that pellets from the young drop to the ground below the nest. Aware of this, I can now explain why some nests accumulate as many as 70 to 100 pellets, while others accumulate only 10 to 20. In every case where I found a large sample, the nest was in an isolated willow bush, in the branches of which the young must have spent several days before venturing across open ground to the nearest continuous stand of brush. In every case where I found few pellets the nest was in a dense stand of brush, into which the young could escape as soon as leaving the nest. So actually the data from samples of shrike pellets collected under nests represent only the foods eaten at the very end of the nestling period.

Tables 5 and 6 present similar data from nests found around Lake Peters in 1959. Note the similarity in composition between these samples and the previous one—all from the same kind of alpine valley tundra. Again and again in these samples from the mountains, the Alaska vole turns up as the dominant rodent in the diet and the Lapland Longspur as the main bird. Generally these are the two commonest vertebrates in the region. Similarly, bumblebees and wasps constitute the principal types of insects eaten. Bumblebees are the commonest and most widespread large insects in arctic Alaska, although locally and irregularly grasshoppers can be more abundant, as at Jago Lake in August 1958 and at Umiat Mountain in July 1959.

TABLE 6

Analysis of 136 Pellets from Five Northern Shrike Nests at Lake Peters, 1959

Species of prey	*Number pellets*	*Per cent frequency*	*Minimum individuals*	*Per cent total individuals*
Water Pipit	1	0.74	1	0.46
Redpoll	5	3.68	5	2.29
White-crowned Sparrow	3	2.21	3	1.38
Lapland Longspur	6	4.41	6	2.75
Snow Bunting	1	0.74	1	0.46
Unidentified bird remains	52	38.24	1	0.46
Total birds	68	50.00	17	7.80
Alaska vole, adults	12	8.82	12	5.50
Alaska vole, juveniles	15	11.03	15	6.88
Tundra vole, adults	3	2.21	3	1.38
Tundra redback vole, adults	4	2.94	4	1.83
Tundra redback vole, juveniles	6	4.41	6	2.75
Brown lemming, adults	1	0.74	1	0.46
Greenland collard lemming (*Dicrostonyx groenlandicus*), adults	1	0.74	1	0.46
Unidentified microtine remains	71	52.21	?	——
Total microtines	113	83.08	42	19.27
Bumblebees	62	45.59	67	30.73
Wasps	7	5.15	12	5.50
Grasshoppers	1	0.74	1	0.46
Ground beetles	62	45.59	79	36.24
Other insects	16	11.76	?	——
Total			218	

TABLE 7

Analysis of 79 Pellets from One Northern Shrike Nest at Umiat, Alaska, 1958

Species of prey	*Number pellets*	*Per cent frequency*	*Minimum individuals*	*Per cent total individuals*
Robin	1	1.27	1	0.58
Gray-cheeked Thrush (*Hylocichla minima*)	1	1.27	1	0.58
Bluethroat (*Luscinia svecica*)	1	1.27	1	0.58
Arctic Warbler (*Phylloscopus borealis*)	1	1.27	1	0.58
Yellow Wagtail (*Motacilla flava*)	9	11.39	6	3.47
Redpoll	2	2.53	2	1.16
Fox Sparrow	1	1.27	1	0.58
Lapland Longspur	4	5.06	4	2.31
Unidentified bird remains	37	46.84	2	1.16
Total birds	57	72.15	19	10.98
Tundra vole, adults	10	12.66	3	1.73
Alaska vole, adults	1	1.27	1	0.58
Total microtines	11	13.92	4	2.31
Bumblebees	64	81.01	131	75.72
Wasps	5	6.33	5	2.89
Carabid beetles	2	2.53	2	1.16
Other beetles	8	10.13	12	6.94
Other insects	5	6.33	?	——
Total			173	

Table 7 shows rather a different picture. This sample was taken from a nesting area in the valley of the Colville River where there are extensive stands of willow and alder brush and where there is a relatively rich and abundant passerine fauna of some 14 nesting species (Kessel and Cade, 1958). Furthermore, most of the sample came not from below the nest but from several feeding stations within a large larder-area, which was being used by a family of fledglings and their parents in the second week of July, a time when many fledgling songbirds were just out of their nests. In this sample, then, birds occurred in 72 per cent of the pellets and made up 11 per cent of the total number of prey, whereas microtines occurred in only 14 per cent of the pellets and made up only 2.3 per cent of the individuals. Interestingly, bumblebees occurred in 81 per cent of the pellets and made up 75 per cent of the total individuals. Bumblebees are easy for shrikes to catch and are among the first sizable quarry to be taken by juvenile shrikes.

TABLE 8

Analysis of 51 Pellets from Two Northern Shrike Nests along the Upper Colville River, Alaska, 1959

Species of prey	*Number pellets*	*Per cent frequency*	*Minimum individuals*	*Per cent total individuals*
Gray-cheeked Thrush	1	1.96	1	1.37
Arctic Warbler	2	3.92	2	2.74
Yellow Wagtail	4	7.84	4	5.48
Redpoll	9	17.65	7	9.59
White-crowned Sparrow	3	5.88	2	2.73
Lapland Longspur	5	9.80	3	4.11
Unidentified bird remains	23	45.09	?	——
Total birds	47	92.15	19	26.03
Tundra vole, adults	2	3.92	2	2.74
Alaska vole, adults	2	3.92	2	2.74
Unidentified microtine remains	21	40.11	?	——
Total microtines	25	49.01	4	5.48
Bumblebees	34	66.66	39	53.42
Carabid beetles	9	17.65	11	15.07
Total			73	

Table 8, summarizing information from two additional nests along the Colville, supports the view that birds constitute a larger fraction of the food in this region than in the mountains. The information from larders also supports this conclusion (compare Tables 9 and 11).

Table 9 summarizes information about all the prey found in the larder-area during the nesting period of a family of shrikes at Lake Peters, an interval of time covering the first 20 days of June 1960. Sixty-three vertebrates were found, of which 18 were birds, 43 were microtine rodents, and 2 were shrews. One significant point of this table is the disproportionate number of male birds taken by the shrikes—15 males to 3 females. The breeding of this pair of shrikes corresponded to the peak period of courtship activities in other small birds that spring, and observations on the hunting tactics of shrikes indicate that they take most adult male birds during their display performances, or, in some cases, when the male tries to distract the shrike from its pursuit of a female (see Cade, 1962, for an instance). No such selective take of males is indicated for the microtines. I hasten to add, however, that, depending on the relative time of reproduction by shrikes in comparison with other birds, a pair of shrikes may also show the reverse specialization and take mainly females at their nests, as is suggested by the data in Table 10.

Tables 9 and 11 list three adult Baird's Sandpipers, all with brood patches, and one adult Semipalmated Sandpiper (*Ereunetes pusillus*). I am reasonably certain that these fast-flying birds were taken by surprise on or

TABLE 9

Vertebrate Prey Found in the Larder-Area of One Family of Northern Shrikes, Lake Peters, Alaska, 1960

Species	*Number*		*Age group*		*Total*
	Males	*Females*	*Adult*	*Juvenile*	
Baird's Sandpiper	3	0	3	0	3
Water Pipit	0	1	1	0	1
Redpoll	1	0	1	0	1
White-crowned Sparrow	0	1	1	0	1
Lapland Longspur	9	1	10	0	10
Snow Bunting	2	0	2	0	2
All birds	15	3	18	0	18
Tundra vole	2	3	4	1	5
Alaska vole	12	15	18	9	27
Tundra redback vole	7	4	11	0	11
All microtines	21	22	33	10	43
Masked shrew (*Sorex cinereus*)	1	1	2	0	2
All prey	37	26	53	10	63

TABLE 10

Vertebrate Prey Found in Larder-Areas of Northern Shrikes around Lake Peters, Alaska, 1959-1963

Species	*Number*			*Age group*		*Total*
	Males	*Females*	*Unsexed*	*Adult*	*Juvenile*	
Water Pipit	0	2	1	3	0	3
Redpoll	1	0	1	2	0	2
White-crowned Sparrow	0	1	2	3	0	3
Lapland Longspur	2	3	0	5	0	5
Snow Bunting	0	2	0	2	0	2
All birds	3	8	4	15	0	15
Alaska vole	10	13	4	23	4	27
Tundra redback vole	5	6	0	8	3	11
All microtines	15	19	4	31	7	38
Masked shrew	0	1	0	1	0	1
All prey	18	28	8	47	7	54

TABLE 11

Vertebrate Prey Found in Larder-Areas of Northern Shrikes along the Colville River, Alaska, 1952[1]-1959

Species	*Age group* *Adult*	*Juvenile*	*Total*
Semipalmated Sandpiper	1	0	1
Bluethroat	0	2	2
Yellow Wagtail	4	11	15
Redpoll	3	1	4
Tree Sparrow	1	5	6
Fox Sparrow	1	0	1
Lapland Longspur	0	8	8
All birds	10	27	37
Tundra vole	2	0	2
Alaska vole	1	0	1
Tundra redback vole	1	0	1
All microtines	4	0	4
All prey	14	27	41

[1] See Kessel and Cade (1958).

TABLE 12

Estimated Total Weight of Food Represented by a Sample of 222 Pellets from Northern Shrike Nests around Lake Peters, 1959

Prey species	*Weight class in grams*	*Number of individuals*	*Total weight*	*Per cent of consumed biomass*
Small birds	25	26	650	21
Young microtines	20	35	700	22
Adult microtines	40	40	1600	52
Shrews	5	1	5	0.16
Bumblebees	0.8	137	110	3.5
Wasps	0.3	34	10	0.32
Beetles	0.2	115	23	0.74
Grasshoppers	1.0	1	1	0.03
Small insects	0.1	10	1	0.03
Totals		389	3100	100

near their nests. It is extremely unlikely that a shrike could fly a sandpiper down in the air.

Summary of Food Habits in Alaska

From these and other data (Cade, unpublished notes), a pattern of seasonal changes in the foods of Northern Shrikes on their breeding grounds in arctic Alaska begins to emerge. When the shrikes first arrive in late April or May (see Irving, 1960), they subsist mainly upon adult passerine birds, taken from the flocks of early arriving redpolls, buntings, and longspurs, with an occasional microtine rodent that has ventured out of the snow cover. As the season progresses, more adult microtines become exposed by the melting snow, and these rodents, along with vulnerable displaying male birds, make up the bulk of food. By late May, the bumblebees are out and are taken at every opportunity through the rest of the season. As soon as the peak period of courtship display is over in the second week of June, the number of songbirds caught by shrikes drops sharply. About this same time, however, the first young voles, weighing 15 to 20 grams, start moving about, and supplement the shrike's diet, although all the pellets so far examined indicate that the shrike continues to catch a greater number of adult voles than juveniles. After the first week in July, fledgling songbirds appear on the tundra, and the adult shrikes, but not yet the juveniles, again heavily prey upon birds.

For the first four or five weeks after leaving their parents, young shrikes subsist mainly on spiders and insects. At first these food items are small, the insects being various ground beetles, flies, and even the mosquitoes that swarm about the shrikes themselves. Soon the young birds are also taking bumblebees and wasps, the commonest large insects that continue as a staple through the summer. Locally, the young shrikes depend heavily on grasshoppers, as evidenced by the foraging of four post-fledgling shrikes at Jago Lake in August 1958. Toward the end of the summer young shrikes begin catching vertebrate prey—mice at first and birds later.

In autumn, both adult and immature shrikes—now as widely spaced, solitary individuals—shadow the large flocks of redpolls, longspurs, and buntings that build up for the fall migration.

Quantitative Aspects of Predation by Shrikes

Contribution of Prey Species to Total Weight of Food

How much does each of the principal kinds of prey contribute to the total weight of food consumed by shrikes during the breeding season? One can obtain an approximate answer by a further treatment of the information provided by pellet analysis. Table 12 lists the principal categories of food eaten by shrikes at Lake Peters in 1959, their average weights in grams, the number of individual animals in each category, the total weight of those individuals, and the percentage composition that each category of prey contributes to the total weight or mass of food.

Thus in 1959, small birds made up about 21 per cent of the total weight of food; young microtines, about 22 per cent; adult microtines, about 52 per cent; and bumblebees—although they made up the largest number of individuals taken—constituted only 3.5 per cent of the total weight. All other insects combined made up only a little more than 1 per cent of the consumed biomass. However, one must remember that the estimation of their numbers in pellets is much less accurate than for larger species. The actual contribution of small insects must be rather larger than the figures in Table 12 indicate; still, I doubt that the actual figure would be more than about 3 per cent.

Amount of Food Consumed by a Family of Shrikes during the Breeding Season

How much food does a family of shrikes consume on its breeding grounds during approximately 60 days of intensive use? To answer this question one needs to know the daily food consumption of a full grown shrike, and also something about the rate of development and the growth efficiency of young shrikes.

Consumption by Adults.—The food consumption of captive shrikes, weighing 65 to 75 grams, averages about 30 grams of whole mouse or bird tissues per day, including the indigestible materials regurgitated as pellets. Since captives expend less energy in activity, this figure, which is about equal to one small bird or mouse per day, can be taken as a minimum estimate of the amount of food required by a wild shrike.

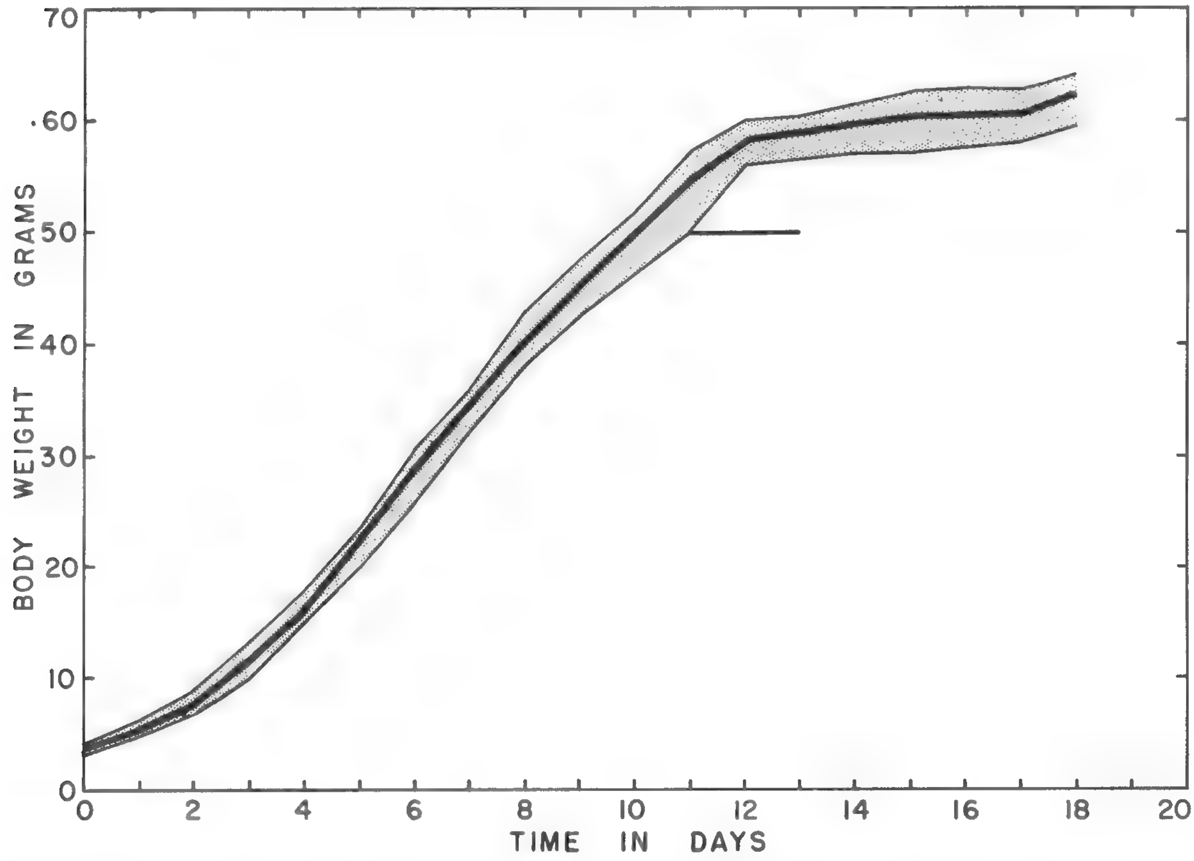


Figure 9. Growth curve for a brood of shrikes from hatching to fledging, Lake Peters, 1959. The heavy line shows the average weight for each day of growth, and the stippled area, the ranges in weights. The number equals 8 through the 11th day of life, 7 thereafter. The last hatched nestling failed to gain weight after the 11th day and disappeared from the nest after the 13th. Weights were recorded routinely at the nest around 8:00 PM each day, except for the initial hatching weights, which were taken as soon as possible after the chicks emerged.

Growth of Nestling Shrikes.—Figure 9 shows a growth curve for a brood of eight shrikes at Lake Peters in 1959. Young shrikes hatch completely naked with a body weight of about 4 grams, and they achieve essentially adult weight in 12 days, having by then gained about 54 grams of additional body weight. While they remain in the nest for another seven to eight days of intensive feather development, they continue to increase slowly in weight and fledge usually on the 19th or 20th day.

Since hatching is usually spread out over three or four days, there is considerable difference in the ages of the young in the nest. It sometimes happens, as shown in Figure 9, that the last one or two hatchlings die before fledging—presumably because they do not get enough food. Because the nest is too small to permit all the nestlings to remain on the bottom as they grow larger, they eventually become arranged in two tiers with the older three or four crouched on top of the younger three or four. If the nest is disturbed as the fledging time approaches, the upper tier of birds may suddenly burst forth and disperse, while the younger birds remain in the bottom of the nest.

Thus, there seem to be two adaptive advantages to the staggered hatching of nestling shrikes. One allows for an adjustment of brood size to fit the optimum feeding abilities of the parents, as dictated by the availability of food for that particular time and location. Lack (1966) discusses this advantage for other kinds of predatory birds. The second advantage may be a mechanism to deflect the attention of nest predators away from the younger siblings when the older ones fly out.

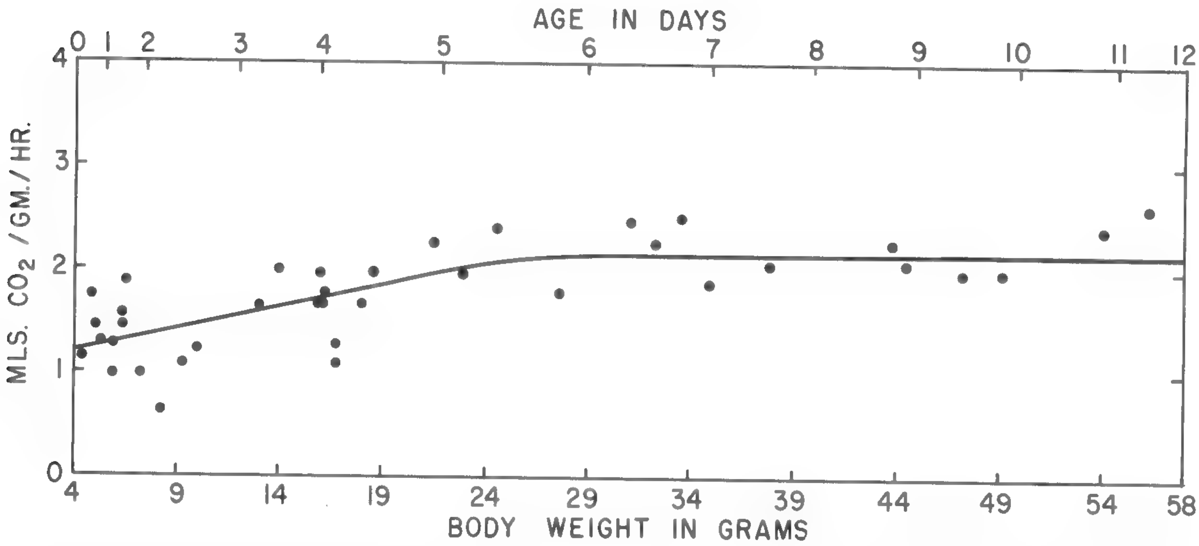


Figure 10. Carbon dioxide production of developing shrikes from hatching to the age of 12 days. Each point represents a measurement made on a single shrike. Ten birds were used. Birds were removed from the nest, fasted 1 to 3 hours; and CO_2 measurements were then made in a Haldane open system respirometer with an air flow of 400 to 500 milliliters per minute. Measurements were made at 35°C during the first 8 days; thereafter, at 30°C. The birds were then returned to the nest. The study was carried out in a field laboratory at Lake Peters in 1963.

Metabolism of Growing Shrikes.—Figure 10 shows the relation of metabolic rate to body size and age in nestling shrikes through the age of 12 days. During the first eight days we took the measurement at an ambient temperature of 35°C, the probable nest temperature of brooded young and one at which they can maintain body temperature above air temperature. Beyond eight days, the young birds began to pant and to show other signs of heat stress at 35°C. Thereafter, we took measurements at 30°C, a temperature at which the young shrikes could maintain body temperatures of 40° to 41°C without panting and which was presumably within the thermal neutral zone.

As in some other altricial passerines (Dawson and Evans, 1960), the metabolic intensity (metabolism per unit of body weight) of the young shrikes gradually increased under ambient conditions approximating those in the nest until the sixth day, after which the metabolic rate remained at a constant level consistent with that predicted for adult birds of comparable size by the new equation of Lasiewski and Dawson (1967) for passerine birds. This means that a young nestling requires less energy for maintenance of bodily functions than does an older one for a given unit of weight. Dawson and Evans (1960) have discussed this finding in connection with the growth efficiency of nestling Vesper Sparrows (*Pooecetes gramineus*), and much of what they say has relevance to the growth of young shrikes, as shown in Table 13.

TABLE 13

Calculation of Food Requirement for a Growing Northern Shrike

Age in days	*Geometric mean weight*	*Metabolic rate kcal per day*	*Metabolic rate as gms per day*	*Growth in gms per day*	*Total net energy as gms per day*	*Growth as per cent net energy*
1	5.0	1.01	0.51	1.50	2.01	75
2	6.5	1.42	0.71	2.00	2.71	74
3	9.8	2.44	1.22	4.50	5.72	79
4	14.0	3.71	1.86	4.00	5.86	68
5	19.0	5.93	2.97	6.00	8.97	67
6	25.0	8.19	4.05	7.00	11.05	64
7	32.0	10.48	5.24	6.00	11.24	53
8	37.5	12.29	6.15	5.00	11.15	45
9	42.5	13.92	6.96	5.00	11.96	42
10	47.5	15.56	7.78	5.00	12.78	39
11	52.5	17.20	8.60	5.00	13.60	37
12	56.5	18.51	9.26	3.00	12.26	24
Total					109.31	

For those unfamiliar with the terms used in Table 13, the geometric mean weight is the average weight of a growing shrike for a given 24-hour period (e.g., if the bird weighs 6 grams at 12 noon one day and 8 grams 24 hours later, the geometric mean weight is 7 grams). The metabolic rate, expressed as kilogram calories (kcal) per day, has been calculated from the measurements of carbon dioxide production presented in Figure 10, on the assumption that the production of 1 liter of CO_2 is equivalent to 6.5 kcal—about right for both fats and proteins, the principal nutrients in the shrike's food (see King and Farner, 1961). Kilogram calories can be converted to gram equivalents of food on the assumption that 2 kcal equals 1 gram of bird meat (see Brody, 1945; Dawson and Evans, 1960). *Net energy* is that fraction of the total energy intake in the food that is made available for various biological functions, including maintenance and growth, and, in the case of the young shrikes, is equal to the sum of the fasting metabolic rate plus the growth in grams per day.

The growth efficiency, as per cent of total net energy, was highest for the first few days after hatching and is comparable to the figures of 74 and 71 per cent reported by Dawson and Evans (1960) for days 1 and 2 of the young Vesper Sparrows. Growth efficiency of the young shrikes decreased, however, with increasing age.

Estimate of Total Food Intake of Nestling Shrike.—Table 13 shows that during the first 12 days of life the total net energy utilized by a nestling shrike is equivalent to approximately 109.3 grams of food. With this information one can estimate the total amount of food required by a growing shrike. As indicated above, the *net energy* is only a fraction of the *gross energy* intake.

Various losses of energy must be taken into account. For a protein diet, one of the largest of these losses is the so-called *specific dynamic action*—the energy lost as heat incidental to the assimilation and metabolic processing of the food (see Brody, 1945). For lean meat the specific dynamic action represents about 30 per cent of the total *metabolizable energy,* and the net energy therefore equals 70 per cent of it. This means that for a net energy equivalent to 109.3 grams of food, the shrike must metabolize energy equivalent to 156.1 grams. Some energy is lost in the uric acid and other end products of metabolism excreted by the kidneys, so that the metabolizable energy is only a fraction of the *digestible energy*—the actual energy absorbed into the circulatory system from digestion of the food. Similarly, some energy is lost in the feces, so that the digestible energy is always less than the gross energy. A conservative estimate for a shrike, which takes in a large mount of indigestible materials when it eats whole animals, is that the metabolizable energy is about 70 per cent of the gross energy intake. Hence, the gross energy intake of a young shrike during the first 12 days of life must equal at least 222.9 grams of food. Assuming that for the last 8 days of nestling life the young shrike has an energy utilization about the same as an adult, then the total food consumed during 20 days of nestling life equals about 463 grams.

TABLE 14

Calculation of the Amount of Food Used by a Family of Northern Shrikes for 60 Days

Period of breeding season	*Number days*	*Calculation*	*Amount in grams*
Preincubation	14	2 × 14 × 30	840
Incubation	16	2 × 16 × 30	960
Nestling	20	2 × 20 × 30	1200
		7 × 223 + 7 × 8 × 30	3241
Fledgling	10	9 × 10 × 30	2700
Total	60		8941

Calculation of the Amount of Food Used by a Family of Shrikes

Table 14 presents an estimate of the total amount of food consumed by an average family of shrikes—two adults and seven young. Nine thousand grams of food seems to be about the right figure. Although I have gone through a number of seemingly erudite calculations to arrive at this amount, I would not want to leave the impression that I consider the accuracy of the figure much more than an estimate of order of magnitude. Even so, I am surprised that the figure is so large; but I have found no reason to think the estimate is grossly in error.

If 9,000 grams equals the total weight of food removed from the nesting area, then 21 per cent of this total equals about 75 adult birds averaging 25 grams, 74 per cent equals 222 microtines averaging 30 grams, and 3.5 per cent equals about 394 bumblebees averaging 0.8 gram. Are these figures significant in terms of predator regulation of the prey populations? To answer this question one needs to know the size of the hunting area from which the food is removed and also the density of the prey populations.

Population Phenomena

Shrike Territories

Working out the relationship between nesting shrikes and their use of the available environment in arctic Alaska is complicated by a number of considerations—e.g., the limited extent of the nesting habitat, the large areas of terrain unsuited for any kind of use by shrikes, and the sparse, highly variable nature of shrike populations at the northern periphery of the breeding range. For instance, the total area encompassed by nesting shrikes around Lake Peters between 1958 and 1963 is approximately 36 square miles (Figure 2). However, this region of steep, rocky mountain slopes and ridges, with no shrubby vegetation or other suitable cover for shrikes, restricts all the activities of these birds pretty much to the lower slopes and alluvial fans around the margins of the lakes and to the floors of valleys. The lake surfaces also restrict shrikes, but since the birds do hawk insects over the water, I have included the lakes within the usable area. Out of the total of 36 square miles in this region, I estimate that about 14 square miles are usable for hunting by shrikes and 3.5 square miles of willow brush, although widely dispersed, are suitable for nesting. Even so, it is by no means clear that nesting habitat sets a limit on the numbers of shrikes in this region.

I judge that there are at least 20 suitable nesting areas for shrikes in the region covered by Figure 2; yet seven is the largest number of pairs that has bred there in any one year. In 1959, Areas 1, 2, 3, 4, 6, 8, and 9 were occupied; but in 1960 only one pair bred in Area 9. The closest nesting pairs in 1959 were just one mile apart, across the lake from each other in Areas 2 and 9. Some apparently suitable nesting areas were never used during the period under observation.

Because the pairs are so widely spaced, shrikes in arctic Alaska do not keep within exact territorial boundaries around their nests, nor do they always react aggressively towards a strange shrike in the vicinity of their nests. Therefore, it is difficult to establish the precise area of their hunting activities during the nesting period. In 1959, I once found the male of Area 1 (see Figure 2) about one mile south of his nest; and in 1961, in Area 3, I saw an intruding adult, after it had been attacked by the resident pair, fly straight away across the lake to the west and disappear over a high divide headed toward Area 7, where a pair of shrikes had lost their nestlings the day before. (I believe the intruder was one of this pair.) I had this bird in sight with binoculars for about two miles, the longest continuous flight I have seen a shrike make. All other sightings of adults have been closer to their nests, usually less than half a mile.

In 1959, I saw the male of Area 1 attack and kill a longspur near the southwest corner of Lake Peters and then carry it in one continuous flight to its nest one-quarter of a mile away (Cade, 1962). This is the farthest distance I have seen quarry transported by a shrike.

In three cases where I watched the daily activities of shrikes during the entire nestling period at Lake Peters (twice in Area 2 and once in Area 9), I estimated the area of major hunting activity for the male to be on the order of half a square mile or 320 acres. I am now convinced that the hunting area is proportional in size to prey densities within some limits, but I doubt that a hunting shrike ever ranges regularly over as much as a square mile during the nesting period.

Even taking into account the rather large area needed by a pair of shrikes for foraging during the nesting season, I still feel that the environment around

Lake Peters should be able to support about 14 pairs of shrikes, allowing a generous square mile of optimum habitat per pair. In other words, during my period of observation, shrikes never used more than half of the environment that is potentially available to support breeding pairs, and in most years they have occupied considerably less than half. I am forced to conclude that it is not the nesting habitat or any other feature of the environment used during the breeding season that limits numbers of shrikes in arctic Alaska. This conclusion applies even more to a region like the Colville River Valley, where suitable nesting habitat is much more extensive than around Lake Peters, yet where breeding shrikes are extremely sparse.

Prey Populations

Bumblebees and Wasps.—Unfortunately, since I have never tried to census bumblebees or other insects in the areas where shrikes occur, I can only offer some general impressions about their numbers. Bumblebees of several species are quite common along the Colville River, and I expect that 10 to the acre would be the right order of magnitude for densities around Umiat, Alaska; certainly they do not reach densities as high as 100 to the acre. Paper wasps are also fairly common in the willow and alder brush, and their nests occur at regular intervals along the rivers and creeks. At Lake Peters the numbers of these insects are considerably less, although they are still the commonest large insects. Wasp nests are infrequent—less than one per linear mile of streambed—and my impression is that active, foraging bumblebees would not average more than one or two per acre. Assuming that these figures are approximately correct, then a pair of shrikes with a hunting area of 320 acres could remove most of the bumblebees in their area.

Individual bumblebees are highly mobile—I have seen them fly across Lake Peters many times—and forage far afield, but they nest colonially in groups of a dozen or more adults. In early spring, the large, overwintering queens are snapped up by the shrikes. Later on, as the queens become sedentary in their nests, the worker bees are hardest hit. Because of the hunting tactics of shrikes, particularly their persistence in returning to a place where they have seen prey disappear, I am sure that before the summer is over the shrikes can eradicate any nesting colony of bumblebees established on an area where they regularly hunt.

In the case of bumblebees, I have no direct observation of this kind of selective predation, but in 1958 at Umiat I did witness the gradual demise of a colony of paper wasps. The wasp nest, a few yards from a shrike nest when I first found it in early July, was in the dead center of a large larder-area used by a family of four recently fledged shrikes and their parents. The wasp nest, a large one about the size of a football, appeared to have only about 15 to 20 workers flying in and out, as nearly as I could tell by disturbing the nest with a stick. A few days later I found no indication of wasp activity and the nest, when opened, contained many dead larvae and some pupae. Since many of the shrike pellets picked up in this area contained remains of wasps, I have no doubt that the shrikes systematically hunted this nest until they caught every adult.

Microtine Rodents.—I can say something more definite about voles and lemmings. Although all five species of microtines occurring in arctic Alaska have been identified as food of the Northern Shrike, the Alaska vole and tundra redback vole (*Clethrionomys rutilus*) are the two typically associated with the brushy habitats where the shrikes do most of their hunting, and are the two most frequently taken. The two lemmings and tundra vole (*Microtus oeconomus*) usually occur in the more open tundra with low vegetation, such as the ground between Lake Peters and Lake Schrader and the lower half of the large alluvial fan on the south side of Schrader (see Figure 2), areas which lack shrubby cover for shrikes.

Without going into the evidence, which consists of unpublished trapping data, let me say simply that in spring, when the snow melts off, average densities of 5 voles to the acre are reasonable for the region around Lake Peters (lower mountain slopes and alluvial fans). This means that the spring population of voles on the 320 acres used by a pair of shrikes is about 1,600 animals. Locally, densities may go as high as 10 voles per acre, and over considerable areas of poorly vegetated rocky habitat, as low as 1 per acre. By August, the densities can be as high as 75 to 100 voles per acre, as on some of the rich alluvial fans along the Okpilak River in 1958 (F. A. Pitelka and Cade, unpublished).

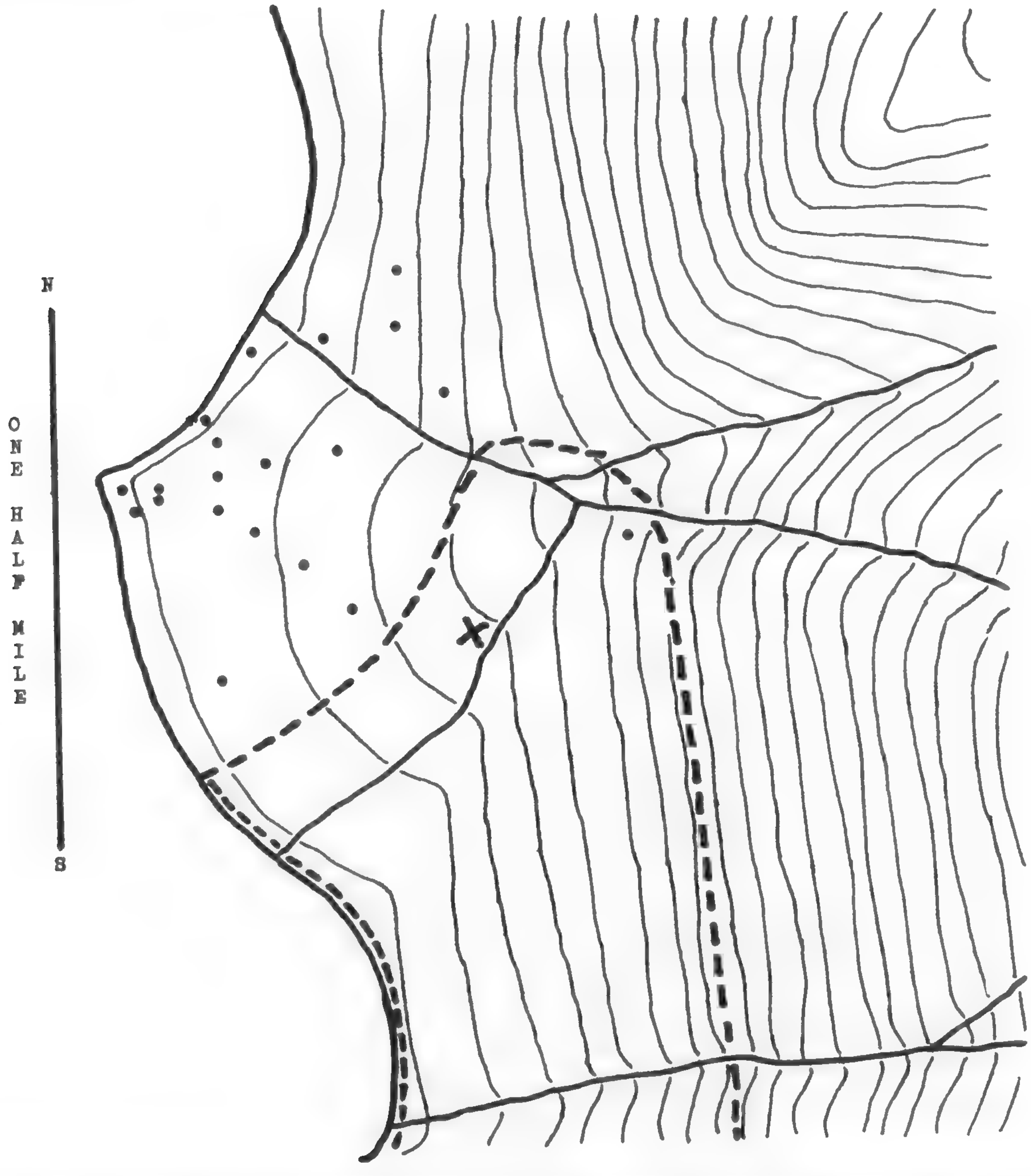


Figure 11. Nesting Area 2 at Lake Peters in 1961. X marks the site of the shrike nest, and the heavy dashed lines indicate the approximate hunting area, which also extended about one-quarter of a mile south of the region shown. Dots show the locations of other nesting birds. Contour intervals are 100 feet (based on a provisional map of the USGS).

By the end of June, the shrikes will have removed approximately 14 per cent of this population, most of this predation occurring before the minimum spring density of voles has been augmented by the current crop of young animals. Nearly every female vole caught by shrikes in the early part of the breeding season is either pregnant or lactating, so that the potential loss to the rodent populations is greater than one individual. Young voles first begin to appear in the shrike's diet around the middle of June. Further, when one stops to consider that other predators—red foxes (*Vulpes fulva*) and especially least and shorttail weasels (*Mustela rixosa* and *M. erminea*)—are also hunting voles on this same area, predation looms as a factor of major importance in the spring mortality of microtine populations—at least in localized areas where predators are concentrated for one reason or another, such as on alluvial fans offering good cover for shrikes and weasels.

Small Birds.—The most unexpected finding of my study is the terrific impact a pair of shrikes exerts on the nesting of other small birds—especially other brush-inhabiting species such as (American) Robins (*Turdus migratorius*), redpolls, Fox Sparrows (*Passerella iliaca*), and White-crowned Sparrows. I have never found other birds nesting successfully closer than 200 yards from a shrike nest, and usually the radius of avoidance is greater.

Figure 11, an enlargement of nesting Area 2 on one of the alluvial fans at Lake Peters, depicts a situation I worked out in detail in 1961. The 100-foot contour lines show that the land slopes upward abruptly to the east. The willow brush is restricted to the upper part of the fan where the stream divides and to the banks of the southwestward flowing branch.

The shrikes' nest is indicated by the X-mark, and the dashed line shows the approximate limits of the hunting area, roughly half a square mile. The northern and northwestern limits of this area were quite rigidly fixed, apparently by the reluctance of the shrikes to range into this open area very far from the willows. Most of the hunting activity was carried out south of the nest-site along a steep, rocky and shrubby slope which has a lot of good cover for shrikes and also gives them the advantage of a downhill flight to the nest when carrying heavy quarry. The only other birds nesting in the area used by the shrikes were a pair of Snow Buntings with a well-concealed nest in a crevice on the face of a precipice in a steep-walled drainage just at the periphery of the shrikes' range and about a quarter of a mile from the shrikes' nest.

In the adjacent, open area of about 200 acres immediately north of the hunting domain, I found 19 nests, including those of Baird's Sandpipers, Water Pipits, Horned Larks, White-crowned Sparrows, Lapland Longspurs, and Smith's Longspurs (*Calcarius pictus*). They represented virtually the total breeding bird population on this 200 acres—not a very high nesting density. The total bird population, however, may have been about twice that—roughly 75 birds—because this area always has a large, transient, non-breeding segment in the bird populations.

In 1960, when shrikes did not nest in the stand of willow brush on this alluvial fan, a pair of Robins nested there, several pairs of redpolls and White-crowned Sparrows, in addition to longspurs, larks, and sandpipers on the immediately adjacent open ground. In 1962 and 1963, the shrikes nested again but lower down the drainage about 200 yards from the lake.

Some of the details for 1963 are pertinent. On 4 June, the shrike nest contained six young and two eggs. Other passerines were in courtship, building nests, or just beginning to lay. E. J. Willoughby and I made a thorough inspection of the alluvial fan and again could find no other birds with territories or nests in the willow brush, but in the open area to the north and west of the willows there were three or four pairs of Water Pipits, four or five pairs of Lapland Longspurs, four or five pairs of Smith's Longspurs, and two pairs of Baird's Sandpipers, in addition to several other birds that did not appear to be stationary on the fan. On 7 June, the shrikes' nest was depredated and torn down, probably by a red fox, and the adult shrikes had departed. A census of stationary birds carried out on 8 and 9 June on the alluvial fan yielded two pairs of Baird's Sandpipers, three pairs of Water Pipits, one pair of Wheatears (*Oenanthe oenanthe*), one pair of Horned Larks, five definite pairs and eight additional displaying males of the Lapland Longspur, and seven pairs of Smith's Longspurs. The Horned Larks, three pairs of Smith's Longspurs, and two pairs of Lapland Longspurs had already moved into grassy areas immediately adjacent to the willows where the shrike nest had been. Still later in the season, some redpolls settled to nest in the willows, and White-crowned Sparrows and Wheatears moved into the steep shrubby slope south of the nesting area.

In other places, I have found redpoll nests in the same willows with old shrike nests, and I once found a pair of Robins with their typical mud-walled nest constructed inside an old shrike nest. I call attention to these details to show that other birds do use the shrike areas when the shrikes are not present.

Wherever they settle, shrikes appear to render about 320 acres of prime nesting habitat marginal for breeding by other passerine birds. This results in part from direct predation and in part from the simple avoidance of the area by other small birds. Shrikes usually begin nesting earlier than other small birds in the Arctic, and, until their own eggs are laid, they make themselves conspicuous on their areas. For the most part, arriving males of other species simply do not set up territories near a pair of shrikes. Those males which establish territories peripheral to a shrike area are exposed to a high probability of capture. If such a male songbird does survive long enough to secure a mate and start nesting, his female is almost certain to be captured while attending to her nest, because shrikes are such persistent and excellent trackers of their prey; and as previously mentioned, they have good memories and will return repeatedly to places where they have once seen prey. Because of this persistent type of hunting, small, stationary birds are highly vulnerable to capture by shrikes; and because breeding bird populations are sparse in this region, a pair of shrikes, according to my figures derived from pellet analysis, seems capable of removing by direct predation, during their breeding period, a number of birds equivalent to the average breeding population on 200 to 300 acres of ground around Lake Peters. This means that in 1959 seven pairs of shrikes probably reduced the willow brush habitat, available for breeding by other passerines, from 3.5 square miles to one square mile.

In conclusion, I feel there is now good evidence that Northern Shrikes exercise a definite control on the numbers and on the breeding distribution of other small bird species with which they come in contact locally on their breeding areas and that they are responsible for a significant fraction of the total mortality occurring among localized spring populations of voles. Shrikes may also exercise some control on bumblebee and wasp populations, at least to the extent that they render certain areas marginal for the survival and reproductive success of these social insects.

Factors Limiting the Shrike Populations

Although a pair of Northern Shrikes may remove a considerable fraction of the prey populations on its breeding area, the fact remains that large sections of the brushland habitat favored by shrikes are not included in the hunting domain of any pair. Over-all abundance of prey, then, could hardly be considered a factor limiting the number of shrikes that nest in northern Alaska. A low density of prey on a shrike's hunting area might influence the success of reproduction; but I have no evidence to suggest that this is frequent in arctic Alaska. The feeding conditions around Lake Peters in 1960, when only one pair of shrikes bred, were not conspicuously different from those in 1959, when seven pairs bred; and the one pair which did breed raised eight young.

The shrikes in arctic Alaska do not have to contend with competing species for their food. While it is true that other avian predators in the foothills—the Gyrfalcon (*Falco rusticolus*), Peregrine Falcon (*Falco peregrinus*), Rough-legged Hawk (*Buteo lagopus*), Short-eared Owl (*Asio flammeus*), Long-tailed Jaeger (*Stercorarius longicaudus*), and Parasitic Jaeger (*Stercorarius parasiticus*)—prey on small birds and microtines, none of these species can be considered ecologically similar to the Northern Shrike, because not one hunts regularly within the brushland habitat occupied by the shrikes. The red fox and two species of weasels hunt for mice and birds in the brush, but passerine birds, generally, are a little exploited category of prey in the foothills of the Arctic Slope.

Furthermore, the environment of northern Alaska does not appear to be marginal for shrikes in respect to vegetation, physiography, or climate. Breeding success is consistently high—the modal clutch size is eight eggs and the average number of fledged young per successful nest is five to six. Why, then, are shrikes not more abundant in arctic Alaska? How and where does limitation on their numbers occur?

The usual winter range of the Northern Shrike barely extends into the northern portion of the regions where wintering populations of small birds are numerous. Over most of their winter range, the shrikes encounter sparse populations of a few hardy northern forms such as chickadees (*Parus* spp.), redpolls, Pine Siskins (*Spinus pinus*), grosbeaks, and buntings. Moreover, the snow cover in its winter range provides a safe haven for its microtine prey, members of which seldom venture onto the surface of the snow for more than a few seconds at a time. Insects, too, are absent. A sparse, irregularly distributed population of passerine birds must provide the bulk of the shrikes' food during the winter. I believe that the general paucity of passerine bird populations on the winter range sets up the conditions for intraspecific competition for food and, therefore, that regardless of how many pairs of shrikes breed or how good breeding success may be, the severity of this winter food shortage basically determines the numbers of shrikes which survive to breed on the summering grounds. This conclusion leads me back to a final consideration of the winter emigrations of shrikes.

I envision these emigrations as resulting from the following sequence of events. While the microtine densities have little effect on the breeding density of shrikes or on the productivity of young shrikes to a stage of independence from their parents, at least in arctic Alaska, they do affect the number of young shrikes that survive to the onset of winter. Young shrikes, because they are poor bird hunters and because insects are gone from the northern districts by the end of September, must depend on microtines. In good microtine years, then, the fall and early winter shrike population may be three or four times greater than in other years. When heavy winter conditions set in, the microtine rodents—regardless of whether a crash has occurred or not—become relatively inaccessible as prey for shrikes. The latter are then forced to turn to sparse populations of small birds for their livelihood. The result, in a year of unusually high survival of the post-fledgling juveniles, is severe intraspecific competition for the sparse food stocks and the consequent forcing of many of the supernumerary birds southward out of the more typical winter range. I further believe that a very large percentage of these shrikes that move far south into the United States are birds of the year, the less successful in competition for food on the northern wintering grounds.

The emigration phenomenon, from my point of view, results from the movement of a surplus winter population that is largely doomed to die before it can contribute to the breeding effort of the spring following. Some emigrants do survive, however, and augment breeding numbers to an extent, but not enough to bring the breeding populations anywhere close to a saturation of the potentially usable habitats in the Far North.

Summary

The predatory habits of the Northern Shrike or Great Grey Shrike (*Lanius excubitor*) have been little studied in North America. I have based the following analyses of behavior and conclusions regarding the significance of predation by shrikes on observations made around 27 nests in northern Alaska in the years 1952 and 1956 through 1963, on an examination of more than 200 carcasses of prey hung in shrike larders and 500 pellets collected around nests, on observations of hunting shrikes during the winter around Syracuse, New York, and finally on experimental studies of 21 captive shrikes.

The Northern Shrike hunts either by watching and waiting for prey from a high perch and swooping down on its intended quarry, or by moving actively about among the branches of trees, through bushes, or on the ground in apparent attempts to flush quarry into flight. The Northern Shrike usually catches small birds in its feet, although sometimes it strikes them down first with its beak; it always attacks rodents first with the beak and kills them before picking them up in the feet. The Northern Shrike will fly to attack small birds and mammals from a distance of at least 200 yards, and bumblebees from at least 100 yards. This shrike is a persistent hunter and spotter; it will return repeatedly to specific locations which it has learned to associate with the activities of prey, such as mouse holes, bird nests, and wasp nests.

The Northern Shrike always kills vertebrate prey by a series of hard bites which are directed to the neck and which sever the cervical vertebrae or damage the nerve cord in the spaces between articulating vertebrae. Like falcons, which kill the same way, shrikes have conspicuous tomial "teeth" in a position just posterior to the hooked tip of the upper bill. This convergence of structure and behavior in falcons and shrikes suggests that the teeth play a role in the killing mechanism.

An examination of remains in pellets and of carcasses hung up in larders near nests in mountain locations of northern Alaska—such as Lake Peters—shows that microtine rodents, mainly the Alaska vole (*Microtus miurus*) and the tundra redback vole (*Clethrionomys rutilus*), make up 20 to 30 per cent of all individual prey taken, while small birds—chiefly the Lapland Longspur (*Calcarius lapponicus*)—constitute only 4 to 8 per cent. In the northern foothills along the Colville River, however, small birds of several species make up 10 to 25 per cent of the prey, while microtine rodents constitute only 3 to 5 per cent.

The data from Lake Peters indicate that small birds compose about 21 per cent of the total biomass consumed by shrikes during the nesting period; young microtines, about 22 per cent; adult microtines, about 52 per cent; and bumblebees, about 3.5 per cent. It is difficult, however, to estimate accurately the contribution of small insects.

From information on adult food consumption and energy requirements for the development of a young shrike, I calculate that the total amount of food used by a family of two adults and seven young during the 60 days from the arrival of the parents to independence of the young is about 9,000 grams, equal to 75 adult songbirds, 222 microtine rodents, and 394 bumblebees, plus odds and ends of other insects.

Pairs of shrikes are widely spaced in arctic Alaska, and they do not keep within exact territorial boundaries. In three cases, where I made detailed observations during the entire nesting period, the hunting area appeared to be on the order of half a square mile. If bumblebee populations average one or two to the acre, then a pair of shrikes will remove most of the bees foraging on their hunting area. If spring vole populations average five animals to the acre, then the shrikes will remove 14 per cent of this population before the rodents have had time to augment their numbers by a significant amount of reproduction. It also appears that a pair of shrikes can remove by direct predation a number of adult birds equal to the average breeding population present on 200 to 300 acres around Lake Peters.

There is little to suggest that the sparse breeding population of shrikes in arctic Alaska is limited by any physical or biotic feature of this northern environment. The main limiting factor on numbers of shrikes is probably winter food shortage—or the relative unavailability of foods in winter.

When the microtine populations crash or become protected by snow cover, the shrikes are forced to concentrate on sparse populations of small birds, and the resulting competition forces many birds of the year south out of the more usual winter range.

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FACTORS AFFECTING THE OCCURRENCE OF THE EURASIAN LAPWING IN EASTERN NORTH AMERICA

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Weather maps by John H. Conover

The Lapwing (*Vanellus vanellus*) is a large Palearctic plover which breeds in northern and central Europe and in Asia. The portion of its wintering grounds with which we will be concerned includes England, Wales, and Ireland, and adjacent areas of the European Continent. As summarized by Bull (1964), this species has occurred accidentally "in the western Atlantic region from Greenland and Baffin Island to the Bahamas and Barbados."

In North American ornithological history, the Lapwing is known mainly for the remarkable trans-Atlantic flight of December 1927 (Witherby, 1928; Ingersoll, 1928; Whittle, 1928; Bent, 1929; Austin, 1929; and John B. May (*in* Forbush, 1929)), when hundreds of these birds reached Newfoundland, while others appeared in Labrador, New Brunswick, and Nova Scotia, and single specimens were obtained in Quebec Province and Maine. Far less spectacular, but still ranking second only to the 1927 phenomenon, was a small trans-Atlantic flight in January 1966, when some 30 Lapwings were recorded in the vicinity of the Gulf of St. Lawrence (Christie and Emery, 1966).

I first learned about this flight through the kindness of several Canadian ornithologists, whose enthusiasm in reporting the details prompted an investigation which led to this paper. Before we examine the flights of 1927 and 1966, we should see them in their historical context.

The Lapwing's History in the New World

If we disregard records for Greenland, where Salomonsen (1950) called this species a "casual visitor," the Lapwing's history in the New World is represented by the records for the 84-year period of 1883-1966 which appear in Table 1. While I shall acknowledge, below, the contributions of many persons to this paper, I wish to express here my thanks to James Bond, Geoffrey Carleton, David A. Cutler, Thomas Davis, Mrs. Phyllis Dobson, Fred T. Hall, Dr. and Mrs. Leslie M. Tuck, and David B. Wingate for their generosity in providing data which do not appear in the literature, and to John Bull, Brina Kessel, and W. Earl Godfrey for their kindness in allowing me to report errors which they have detected in the published record.

A few comments on the historical record are in order here. In discussing Lapwing occurrences in the New York City area, Bull (1964) mentioned three records for Long Island: Merrick, 27 December 1883; Mecox Bay, late fall

TABLE 1

Lapwing Records in the New World

Year	*Date*	*Area*	*Number*	*Authority*
1883	27 December	Long Island, New York	2 (1*)	Dutcher (1886) Bull (1964)
1886	24 December	Barbados	1*	Witherby (1928) Bent (1929)
1897	17 March	Nova Scotia	1 (dead)	Piers (1898) Tufts (1962)
1900	November	Bahamas	1*	Fleming (1901) Bent (1929)
1905	Late fall	Long Island, New York	1*	Beebe (1906) Bull (1964)
1905	23 November	Newfoundland	1*	Brewster (1906) Peters and Burleigh (1951)
1905	12 December	Nova Scotia	1*	Tufts (1962)
1917	January	Labrador	1*	Bent (1929)
1926	October	Baffin Island	1*	Godfrey (pers. commun.)
1926	12 November	North Carolina	1*	Brimley (1927)
1927	December	Newfoundland, Labrador, New Brunswick, Nova Scotia	Great flight	To be discussed
1927	*ca.* 15 December	Quebec Province	1*	Taverner (1929)
1927	21 or 22 December	Maine	1*	May *in* Forbush (1929) Palmer (1949)
1932	20 November	Rhode Island	1*	Dickens (1934)
1940	3 December	South Carolina	1	Sprunt and Chamberlain (1949)
1940s	?	Bermuda	1	Hall (pers. commun.)
1944	19 November	Newfoundland	1*	Peters and Burleigh (1951)
1953	14-15 March	Delaware	1	Cutler (pers. commun.)
1953	16 March	New Jersey	1	Cutler (pers. commun.)
1955	7 January	Newfoundland	Adult male*	Tuck (pers. commun.)
1956	December	Bermuda	Small flock	Wingate (pers. commun.)
1957	3 January	Bermuda	1	Wingate (pers. commun.)
1959	late September	Newfoundland	A few	Tuck (pers. commun.)
1959	3 October	Newfoundland	1	Tuck (pers. commun.)
1960	14 January	Newfoundland	Several (1*)	Tuck (pers. commun.)
1960	30 January	Newfoundland	1 (dead)	Tuck (pers. commun.)
1963	25 July	Barbados	Male*	Bond (pers. commun.)
1966	January	Eastern Canada; Isles St. Pierre et Miquelon	Small flight	To be discussed

TABLE 1 (cont.)

Year	*Date*	*Area*	*Number*	*Authority*
1966	26 February	Nova Scotia	1	Dobson (pers. commun.)
1966	25 October	St. Pierre et Miquelon	1*	Tuck (pers. commun.)
1966	3-18 December	Long Island, New York	1 (photographed)	Bull, Carleton, T. Davis (pers. commun.)
1966	26 December	Bermuda	1	Wingate (pers. commun.)

*Specimen collected.

1905; and Bridgehampton, 1910. In 1967, however, Bull (pers. commun.) wrote: "In re-evaluating the Long Island occurrences of the Lapwing for the years 1905 and 1910, I am convinced that the two published accounts (*Auk,* 6: 221, 1906) and (*Auk,* 56:332, 1939) refer to one and the same bird. The great similarity in the localities, dates, and especially the names of the collectors mentioned, leads me to believe that only the 1905 record should stand."

Ingersoll (1928), Witherby (1928), Bent (1929), and May (*in* Forbush, 1929) said that a Lapwing specimen was obtained on Baffin Island in October 1927. But W. Earl Godfrey (pers. commun.) has shown convincingly that this specimen, which is in the National Museum of Canada collection, "was shot at Pangnirtung, Baffin Island, in October 1926, *not* 1927."

Although Bent (1929) said that *Vanellus vanellus* had been recorded casually in Alaska ("small islets in Norton Sound"), Brina Kessel (pers. commun.) wrote that she knew of no reliable records of this species in that state, adding: "Gabrielson and Lincoln, in their 'Birds of Alaska,' list one questionable record, and I know of none since."

The literature contains no Lapwing records for Delaware or New Jersey. However, David A. Cutler (pers. commun.) wrote that, on 15 March 1953, he saw a Lapwing, originally found on the preceding day by John Miller and Charles Price, on the outskirts of the Bombay Hook Wildlife Refuge, Delaware. Cutler observed the bird at close range as it fed with a flock of Killdeer (*Charadrius vociferus*) during a severe rainstorm. When the bird was flushed, it flew eastward toward the Delaware River, uttering its characteristic call. Cutler added that the late Dr. John Arnett informed him that, on the next day, 16 March 1953, he observed a Lapwing in New Jersey in an area across the Delaware River from Bombay Hook.

A similar possibility that the same bird may be involved in two separate records arose in late 1966. The weather maps suggest that the Lapwing, present on Long Island, New York, during 3–18 December 1966, may have been the same individual which Wingate saw at Bermuda on 26 December 1966.

Finally, confusion may arise over recent records of "lapwings" in Florida. In personal communications, C. Russell Mason, William B. Robertson, Jr., and Henry M. Stevenson each told me that all of these Florida records refer to the South American Lapwing (*Belonopterus chilensis*), not to *Vanellus vanellus* (see Northup, 1962).

Turning to the data in Table 1, we see that, except for the male which was collected in Barbados in July 1963, all New World records of the Lapwing fall within the period of September-March. But the great majority of occurrences have been concentrated in the late-fall, early-winter months: November, December, January. This *seasonal* concentration, moreover, combines with a *geographical* concentration. Most of the records are from eastern Canada; and Newfoundland emerges as the focal point. Indeed, the tendency of these birds to appear in the vicinity of the Gulf of St. Lawrence contrasts with the scarcity of Lapwing data along the Atlantic coast of the United States, where a century of active coverage by gunners, collectors, and bird watchers has yielded only nine records for the entire area from Maine to South Carolina, inclusive. It is relevant to this discussion that there are only two records for all of New England (Aroostook County, Maine; Block Island, Rhode Island), which is immediately adjacent to the Maritime Provinces of eastern Canada. *Vanellus vanellus* does not appear, even hypothetically, in the several avifaunal books dealing with such a center of avid bird-seeking as Massachusetts (see, for example, Griscom and Snyder, 1955, and Hill, 1965).

The Lapwing as a Migrant

Eugene Eisenmann (pers. commun.) has pointed out that this bird "is not highly migratory"—i.e., in the sense that the American Golden Plover (*Pluvialis dominica*) is a long-range migrant. Thomson (1926) made this same point about the Lapwing, contrasting it with species "which perform long journeys extending beyond the Equator." Thomson specifically described *Vanellus vanellus* as "a species which is represented throughout the year in a large part of its range and of which some individuals are probably stationary: nevertheless, complicated movements on a great scale take place and in some cases the individual journeys are of considerable length." In its tendency to winter within a portion of its breeding range, the Lapwing might be compared to the Killdeer as a short-range migrant. It is an intriguing coincidence, if not actually a point of some relevance, that in late-November 1888 the Killdeer was involved in an over-water flight, from the vicinity of the Carolinas to coastal areas of New England and the Canadian Maritime Provinces (Chadbourne, 1889), which was somewhat analogous to the trans-Atlantic flights of Lapwings.

All this is by way of establishing the fact that, in our consideration of Lapwing occurrences in the New World, we are concerned with over-water flights of some 2,000 miles, performed by a species which normally does not travel long distances. This point leads inevitably to several questions. *Where* did the Lapwings come from, particularly in 1927 and 1966, to reach eastern North America? *Why* do the trans-Atlantic flights of this species tend to occur in November, December, and January? *What* carries the birds *westward* over an ocean normally ruled by moderate to strong west winds? *How* are the Lapwings directed to particular landfalls, especially in the vicinity of the Gulf of St. Lawrence, rather than to nearby areas on the Atlantic coast of the United States? The purpose of this paper is to investigate these questions.

Fieldfares to Greenland

Perhaps only one other recorded phenomenon, involving a similar trans-Atlantic flight of strays from the Old World, has provided opportunities for detailed analysis equal to those to be found in the Lapwing flights of 1927 and 1966. That phenomenon was, interestingly, an event of midwinter. As described by Salomonsen (1950), a hard-weather movement (i.e., an emigration of wintering birds, caused by severe weather) of Fieldfares (*Turdus* *pilaris*) from southern Norway to the British Isles, on 19 January 1937, was intercepted over the North Sea by a southeast gale, which carried many of the birds to Greenland. Fisher and Peterson (1964) published a map, showing how the Fieldfares were driven via Jan Mayen to northeastern Greenland, from whence they moved southwestward, over the icecap, to southwestern Greenland, where this thrush has become established as a breeding species.

The Source of Lapwings Reaching North America

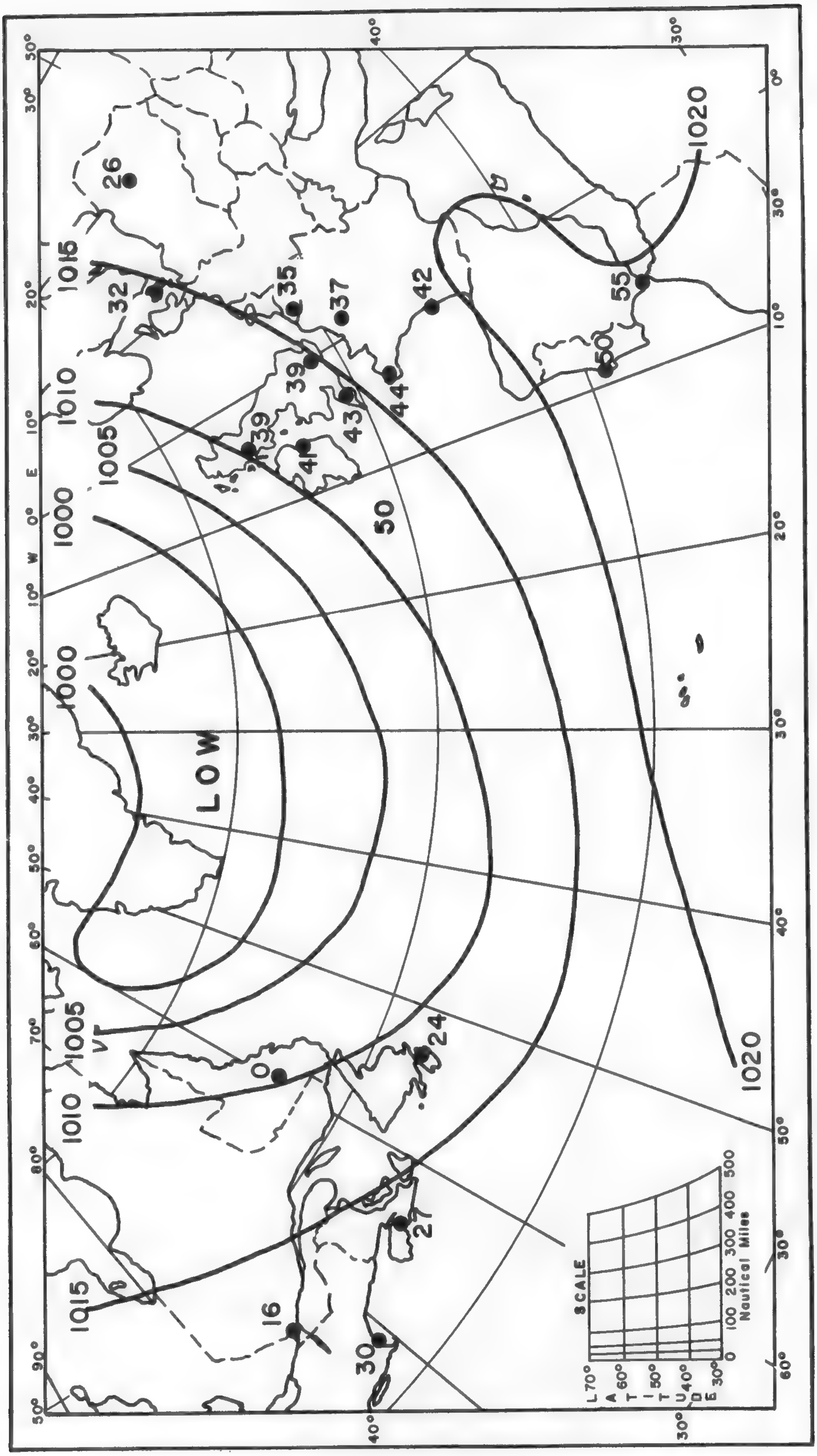
In his analysis of the 1927 flight, Witherby (1928) reported that one of the birds, which was shot at Bonavista, Newfoundland, on 27 December 1927, had been banded as a nestling, in May 1926, at Ullswater, Cumberland, in the Lake District of northwestern England. This fact, combined with a mass of circumstantial evidence both ornithological and meteorological, suggests beyond reasonable doubt that the source of the Lapwings which reached North America in 1927 must be in western Europe, and specifically in the vicinity of England and Ireland. Just a year previously, Thomson (1926) discussed the "complicated movements" which the Lapwings perform in western Europe, both in the usual fall migrations and in the "notable winter movements subsequent to the ordinary migration season." I will speak about these winter movements presently.

For now, it is pertinent that both Thomson and Witherby said that banding had revealed a tendency for Lapwings from northern England and Scotland to appear in Ireland in winter. From his experience as a records editor of the *Irish Bird Report,* R. F. Ruttledge (pers. commun.) told me that in every winter there is an immigration of Lapwings into Ireland, and that banding has shown the earlier arrivals at least (in late September and October) to be from Scotland and the northern half of England. He added that, later in the season, there is banding evidence, in Ireland, of birds of Continental origin—i.e., Lapwings which had been banded in Norway, Sweden, Finland, and Denmark, and which were recovered in Ireland in winter. In 1926, Thomson had said that banding data showed Holland, Denmark, southern Sweden, northern Germany, and Esthonia to be among the source areas for Lapwings visiting southeastern England in winter. By way of summary, Ruttledge wrote: "I am sure that in periods of severe weather on the Continent and in Britain the great numbers [of Lapwings] that flow westward to Ireland come from both origins." From all of this, as Witherby suggested in 1928, Ireland appears to be the critical area in the analysis of trans-Atlantic flights of these birds in late fall and early winter.

Before we pursue this point further, we should consider a question of prime relevance to this investigation: How can this plover winter regularly and successfully so far north as England and Ireland, both of which lie north of Latitude 50° N, as far north as northern Newfoundland and southern Labrador?

Some Climatological Considerations

A North American observer may be surprised to realize that Dublin, Ireland, and Goose Bay, Labrador, are in approximately the same latitude: 53° N. But while Dublin's normal mean temperature in January is 41° F (*cf.* a January mean of 42° F at Norfolk, Virginia), Goose Bay's normal January mean temperature is 0°F! Indeed, Tannehill (1943) stated: "*In corresponding*


LOW
1000
1000
1005
1005
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50
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41
43
42
44
50
55
0
24
27
16
30
SCALE
LATITUDE
70°
60°
50°
40°
30°
0 100 200 300 400 500
Nautical Miles

Figure 1. The mean surface barometric pressure pattern at sea level for January over the North Atlantic Ocean, adapted from Plate XVI, "Climatology," by B. Haurwitz and J. Austin, copyright 1944, McGraw-Hill Book Company, and used with their permission. The mean temperature data (in degrees F) for January at selected stations, from "Weather around the World" by Ivan R. Tannehill, copyright 1943, Princeton University Press, and used by their permission.

latitudes the eastern Atlantic Ocean and western Europe are decidedly warmer in winter than the western North Atlantic and the eastern coasts of North America." This fact becomes evident in the normal January mean temperature data (in degrees F), from Tannehill, which appear in Figure 1 and show that western Europe normally enjoys a relatively mild winter climate. Moreover, the closer an area of western Europe is to the Atlantic Ocean, the milder the winter climate.

This has a two-fold significance as far as we are concerned. First, the Lapwing can winter considerably farther north in western Europe than, for example, the Killdeer in North America. Second, an important factor in the trans-Atlantic flights of the Lapwing lies in this species' reaction to periods of cold weather, in late fall and winter, in western Europe.

The North Atlantic: The Sea and the Air Over It

There are two main reasons why western Europe normally enjoys a relatively mild winter climate. First, the northeastern extension of the Gulf Stream, known as the North Atlantic Current, directs a broad flow of warm water to the coasts of western Europe. This ocean current does not appear in Figure 1, but the reader can find it in an atlas (e.g., the National Geographic Society's "Atlas of the World," 1963). Second, the normally prevailing westerly winds over the North Atlantic in winter carry into western Europe a flow of air which has been warmed by the ocean waters over which it has passed. (In Figure 1, note the 50° F mean air temperature for January over the water just southwest of Ireland.) The nature of this prevailing winter airflow over the North Atlantic will be obvious to the meteorologically informed reader who examines the isobaric pattern in Figure 1. Other persons will need some explanation of the various features in this figure and in the following weather maps in order to understand this paper.

Barometric Pressure Patterns

A weather map shows the barometric pressure pattern which prevails over a given area at a given time. The pattern emerges from the arrangement of isobars—lines that connect points on the map at which, at a given time, the barometric pressure is the same. On modern weather maps, the barometric pressure value for each isobar is given in metric units, *millibars.* (For practical purposes, a value of 1,016 millibars equals 30.0 inches of mercury; similarly, 982 millibars equals 29.0 inches, and 1,033 millibars equals 30.5 inches.) As we can see in Figure 1, these isobaric lines often curve, forming concentric figures of a roughly circular nature. If the pressure values *decrease* inwardly toward the center of such a concentric figure, the isobars outline the contours of a low pressure area, or "Low." If the pressure values *increase* inwardly toward the center, the isobars outline a high pressure area, or "High."

The arrangement of Highs and Lows on a weather map portray the overall pressure pattern prevailing over the area at that time. In looking at the Highs and Lows on a map, we must keep in mind the fact that, in the Northern Hemisphere, air flows in a *clockwise* direction around a *High,* and in a *counter-clockwise* direction around a *Low;* also, that the spacing and orientation of the isobars provide an indication of the speed and direction of windflow in a bottom layer of the atmosphere roughly 3,000 feet deep. In general, wind direction is parallel to the isobars, with low pressure to the left of the observer looking downwind. The speed of the windflow is proportional to the closeness of the isobars. When the isobars are close together, the resulting pressure gradient is said to be "tight" or "steep." As a rule, the tighter the gradient, the stronger the winds in that area. On the Daily U.S. Weather Bureau Maps, the contour interval (i.e., the difference in pressure value between one isobar and the next) is 4 millibars. In Figure 1, the contour interval is 5 millibars. In all other maps accompanying this paper, the contour interval is 10 millibars. The reader should remember this in visualizing the pressure gradient represented by the spacing of the isobars on a given map. For, obviously, when isobars are drawn to indicate pressure differences of 10 millibars, the resulting pressure gradient will not *seem* as tight as it would appear if the isobars were drawn to show pressure differences of 4 or 5 millibars.

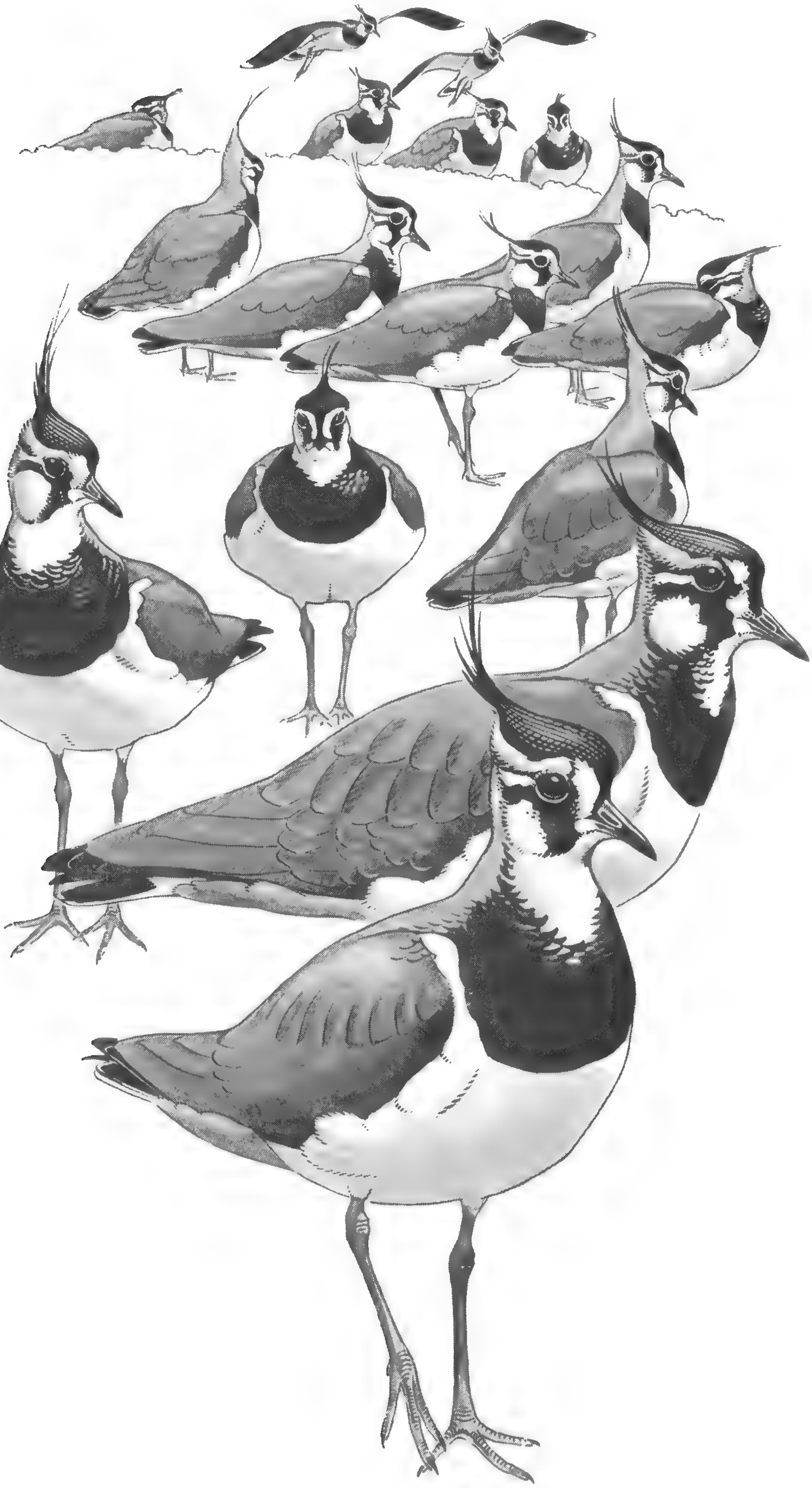
The "Icelandic Low"

Before we consider the abnormal weather situations which have a direct bearing on the flights of Lapwings to eastern North America, we must be aware of the general situation which normally prevails in winter. A particular purpose of Figure 1 is to show the normal mean surface barometric pressure pattern for the month of January, over the North Atlantic (from Haurwitz and Austin, 1944). The pattern in Figure 1 represents an *average*. Variations from day to day may be extreme as Highs and Lows move across the area shown. Nevertheless, what this mean pattern forms is a semipermanent low pressure area, centered southwest of Iceland and known as the "Icelandic Low." It is the prevailing pattern of winter over the North Atlantic. If we think in terms of a counter-clockwise airflow around this Low, with the air flowing virtually parallel to the isobars, we can visualize a river of air streaming southeastward over eastern Canada, eastward over the mid-Atlantic, and northeastward over Ireland and the United Kingdom. Such an airstream, "originating" as cold Canadian air, becomes warmed in its passage over the Atlantic, and enters western Europe as relatively warm air. (Contrast the January mean temperature values at various points in Europe on the one hand, and in North America on the other.) It is this warm airstream which permits the Lapwing to winter in England and Ireland. Moreover, such an airstream clearly will not carry Lapwings across the Atlantic to North America. Therefore, in the December 1927 and January 1966 situations, we will look for significant departures from the mean pressure pattern for winter shown in Figure 1.

Occasionally, a significant change does occur in this prevailing pattern. The westerly (i.e., *from* the west) flow of mild air into western Europe may be cut off, or diverted northward, or may even be reversed. Simultaneously, high pressure may build over Scandinavia. As a result of the *clockwise* airflow around a High centered over Scandinavia, cold continental air masses from the east flow westward out of "the great pool of cold air in the interior of Russia and Siberia" (Tannehill, 1943), invading the Low Countries, the United Kingdom, and Ireland. The effect of such cold-air invasions on Lapwings wintering in western Europe is of primary importance in this discussion.

Hard-weather Movements of Lapwings

Thomson (1926) devoted an entire chapter to the migrations of the Lapwing. After describing the complicated movements which occur in this species' fall migration, in the United Kingdom and Ireland, especially during Septem-



Lapwings. Drawing by Robert Gillmor.

ber, October, and November, he said: "There are also notable winter movements [of Lapwings] subsequent to the ordinary migration season. These movements are, indeed, of a far more general and striking character than the autumnal migrations, but their extent and the time of their occurrence depend entirely on the severity of the season. . . . In severe winters, the weather movements in west-central Europe also give rise to an immigration [of Lapwings] on the southern section of the east coast of England, the birds afterwards spreading westward across the country."

Peter Davis, Migration Officer of the British Trust for Ornithology, has provided (pers. commun.) more detailed and contemporary information on this species' response to cold weather: "This is the normal pattern of Lapwing movement in Britain during the winter: a southwestward shift with the onset of cold easterly conditions, and a return movement with the thaw. Such movements occur repeatedly throughout our winters. The Lapwing is certainly our most sensitive common winter resident as far as cold weather is concerned, and Dr. David Lack's radar studies showed that there is a regular shuttle service [of Lapwings] across the southern part of the North Sea in winter, as well as within Britain." And, as I mentioned above, Ruttledge spoke of the great numbers of Lapwings that flow westward to Ireland in periods of severe weather on the Continent and in Britain. Thus, the Lapwing's response to cold weather is to move westward, into milder areas near the Atlantic Ocean. As one can see in Figure 1, Ireland provides not only the *mildest*—but also the *last*—such area to the west.

Lapwings to Iceland

Now and then these birds get into trouble as they move westward in hard weather. They probably overshoot the coast of Ireland. While we have no actual testimony that they do so, the weather maps provide sufficient circumstantial evidence to justify the belief that offshore (easterly) winds drift the birds seaward, and that many of them then fly downwind, in the direction of the airflow. In such cases, if the airflow is from the southeast and strong, it may drive the Lapwings northwestward, as it did the Fieldfares. However, the southeast winds appear to intercept the Lapwings in the vicinity of Ireland, rather than over the North Sea. Thus, the Lapwings may turn up in Iceland, where there are "numerous records between September and March" (Bent, 1929). Recent testimony on this point came from Finnur Gudmundsson (pers. commun.), who wrote on 24 February 1966: "Practically every winter we get some Lapwings in Iceland—in some years big invasions, but in other years only scattered birds. This winter [1965-1966] no invasion occurred, but one bird was found dead near Reykjavik, 6 February 1966." The relevance of the fact that there was no Lapwing invasion in Iceland at the time of the January 1966 trans-Atlantic flight will become clear when we consider the latter. It appears, then, that winter weather patterns, of such nature as to carry some numbers of Lapwings to Iceland, develop relatively often over the years—far more frequently than patterns which carry them to North America.

The 1927 Flight

Against such background, we now may consider the December 1927 flight. Several discussions of this remarkable phenomenon appeared soon after the event: Ingersoll (1928), Whittle (1928), Witherby (1928), Austin (1929), Bent (1929), Peters (1929), Taverner (1929), and May (*in* Forbush 1929). Subsequently, further information came to light in various provincial, state, and area books: Pettingill (1939), Palmer (1949), Peters and Burleigh (1951), Squires (1952), and Tufts (1962). As far as analysis of the flight was concerned, Ingersoll associated the Lapwings' appearance in Newfoundland with easterly gales occurring at the time, while Whittle related the birds' departure from Europe to strong southeasterly winds. But Witherby provided a masterful interpretation of the flight, based solidly on meteorological information, and I am delighted to follow his account, supplementing the latter with maps which John H. Conover has drawn to illustrate the respective roles played by various weather factors.

Before we turn to Witherby's account, however, I should point out that, when he wrote his analysis, he knew of the birds in Newfoundland but was unaware that in this flight some numbers of Lapwings had reached Labrador. Ornithological news pertaining to Labrador does not readily come to light, and pertinent information on the 1927 flight did not emerge until June 1928, when Austin visited Labrador. Austin learned that Lapwings, including flocks of 10–50 birds, had appeared along that coast as far north as Hopedale, at the time of (significantly) "a spell of exceedingly mild weather during the week before Christmas" 1927. It is true that a footnote, appended to Witherby's paper, mentioned a radio report from Capt. D. MacMillan to the effect that Lapwings had been seen at Anatalok Bay, near Nain, Labrador, on 22 December 1927, and at other places "that week." But in speaking of two Lapwing skins brought back by the Rawson-MacMillan Expedition, Austin said that these birds were shot late in December 1927 near Hopedale ("not Nain"). He added that these two Hopedale skins represented the northernmost records during the flight. Austin himself received a live Lapwing which had survived in captivity from December through June. In addition, an Eskimo woman gave him a Lapwing skin, and he also obtained one skin each of three other Old World birds: a European Coot (*Fulica atra atra*), a European Common Snipe (*Capella gallinago gallinago*), and a European Jack Snipe (*Limnocryptes minimus*). Since these birds had been killed in late December 1927, Austin felt that they had reached Labrador in the same storm that brought the Lapwings. In this connection, it is interesting that, at Exploits Harbour, Newfoundland, in December 1927, three Common European Coots were seen, one of which was collected (Peters and Burleigh, 1951).

From the evidence which he compiled, Witherby concluded that the Lapwings in the 1927 flight began to arrive on this side of the Atlantic on 20 December. Candidly acknowledging that there were reports for earlier dates in December, he said that, if such reports could be proved, they would make the phenomenon more remarkable through their implication that Lapwings had been departing from Europe "independently," over a period of time, rather than in one single group. However, he then stated: "As a working basis I have ignored the rather uncertain records of arrival before the 20th and have assumed that the first birds reached Newfoundland . . . on December 20."

From my advantage of knowing that, in the 1966 flight, there was at least one firm record for a date which was eight days prior to the apparently "logical" date of Lapwing arrival in North America, I believe we should pay some attention to the dates earlier than the 20th in the December 1927 reports. Witherby himself mentioned three reports during 1-19 December. The earliest of these derived from Ingersoll, who had said that, in Newfoundland, the Lapwings "were observed first on December 1," and had implied that some of the birds appeared in Newfoundland during the "second week" of December, in strong easterly storms. Taverner wrote that a Lapwing was taken, "about December 15," at St. Augustine, Saguenay County, Quebec. Peters and Burleigh ignored the report for 1 December; but, apparently using a vague report mentioned by Witherby, said that the first Lapwing of the 1927 flight in Newfoundland "was found at Garnish, December 17." And in Nova Scotia, Tufts stated that several Lapwings were seen near Lower L'Ardoise, Richmond County, from early in December until about Christmas 1927. To sum it up: Considered separately, each of these reports is disturbingly uncertain; considered together, they raise the equally disturbing possibility that, in 1927, some Lapwings *were* arriving in eastern Canada before 20 December. May (*in* Forbush, 1929) suggested that "a small flight of Lapwings" crossed the Atlantic about mid-December.

In any event, both Witherby and Ingersoll provide clear evidence that the major part of this flight began to arrive on 20 December. Testimony contained in one report led Witherby to assume that the first birds reached Newfoundland around 3:00 PM, Atlantic Standard Time (7:00 PM, Greenwich Mean Time) on the 20th. From this, he worked backward to determine the time of departure of the main numbers of birds from Europe. Giving the Lapwings an air speed of 45 miles per hour (mph) and placing them in an airstream flowing *from* the east at 55 mph, he calculated that the birds were achieving a ground speed close to 100 mph. By this reckoning, he felt that they crossed the Atlantic in about 24 hours. From his "approximate estimate," Witherby concluded that "this would bring the hour of starting to 7 P.M., G.M.T., on the 19th." The conclusion appealed to him because (he said) "it is well known that Lapwings start their emigrations after dark."

Regarding the source area from which the birds began the flight, Witherby found a hint in the Lapwing, mentioned above, which had been banded as a nestling in northwestern England in May 1926 and which was shot at Bonavista, Newfoundland, on 27 December 1927. Moreover, he cited the fact that nine Lapwings, banded in northern England and southern Scotland, were recovered in Ireland between 19 December 1927 and the end of January 1928, as evidence of a large movement of these birds from northwestern England towards Ireland at that time. May (*in* Forbush, 1929) said that three observers in England reported seeing flocks leaving the west coast on 18 December, and heading west or southwest. Ingram and Salmon (1934) provided testimony, which seems not to have been available to Witherby, that suggests a more general westward movement; after commenting on the 1927 trans-Atlantic flight of Lapwings, they said: "In South Wales we noted an unusual number of flocks passing west immediately preceding this event, and concluded they were making for Pembrokeshire [the southwestern extremity of Wales] or Ireland."

The next question was: What set off the movement of Lapwings on or about 19 December 1927? Here, Witherby could bring solid facts to bear. He stated that there was a very cold spell, with the temperature remaining below the freezing point day and night, over much of England and Scotland during 16-20 December; he concluded that this set off a hard-weather movement of the type discussed above.

As for the route by which the Lapwings reached North America in 1927, Whittle and Witherby offered differing hypotheses. Whittle suggested that strong southeast winds over western Europe on 16-17 December could have driven the birds to Iceland and Greenland, and that, later, "polar winds and a search for food" forced them to move southwestward to northern Labrador and then southeastward along the coast to Newfoundland where the birds "became gradually concentrated." This hypothesis does not seem plausible.

Witherby's interpretation was that, because the severely cold weather had frozen the ground and food was difficult to obtain, the Lapwings left northwest England about 7:00 PM on the evening of 19 December, bound for central or southern Ireland. He suggested that "this necessity to move happened to coincide with an exceptionally high easterly wind" which carried them beyond the west coast of Ireland. Since the wind velocity was close to, or greater than, the birds' air speed, the Lapwings could only continue downwind in an airflow whose "strength and direction . . . enabled them to reach Newfoundland, 2000 miles away, before exhaustion and starvation brought them down." Witherby had access to meteorological information, and he stated that on the morning of 20 December the wind at approximately 1,000 feet must have averaged 55 mph from almost due east all the way across the Atlantic to within 100–200 miles of Newfoundland.

From the revelations of the weather maps, I believe we can accept Witherby's hypothesis with a few qualifications. First, his determinations regarding the timing and location of the birds' departure seem too narrowly restricted. Some—indeed many—Lapwings may have begun the flight about 7:00 PM on 19 December. However, to anticipate our study of the 1966 flight, we have testimony that flocks of Lapwings were coming in from the east, over the Irish Sea, in the Dublin Bay area of Ireland, all day on 15 January 1966. This suggests that they had started their flights at different times and/or from different places. Moreover, as mentioned above, westbound *diurnal* flights of Lapwings occurred in South Wales in December 1927 on some date which Ingram and Salmon considered relevant to the trans-Atlantic flight. It seems likely that the birds were taking off on hard-weather flights over a period of time during 16-19 December 1927, and from a considerable part of the United Kingdom and nearby areas of the Continent. But it is probable that the main numbers of birds were swept over Ireland, or past its southern extremity, sometime on 19 December.

In the second place, we must remember that Witherby did not have Austin's testimony on the extent to which Lapwings appeared along 300 miles of the Labrador coast, as far north as Hopedale, in the week before Christmas 1927. Newfoundland was, indeed, the focal point of the flight. But Witherby would have modified his interpretation if he had had the Labrador information. The weather maps would have permitted such modification.

The accompanying weather maps show the pressure pattern prevailing over the North Atlantic at 1300 (1:00 PM) Greenwich Mean Time on each day during 18-21 December 1927. Greenwich Mean Time is the local time along the meridian (Longitude 0°) which passes through Greenwich, England. In 1927, Newfoundland and nearby areas of eastern Canada were in the Atlantic Standard Time zone. To convert Greenwich Time to Atlantic Time, subtract 4 hours from the former. Thus, 1300 (1:00 PM) GMT equals 0900 (9:00 AM) AST. There is a 10-millibar pressure difference between one isobar and the next on these maps, which present a few temperature figures in degrees F and wind symbols reflecting observations made at 1300 GMT. The wind symbols show wind direction in the conventional manner; wind speeds are in the Beaufort Scale. We can now examine the 1300 GMT maps for 18-21 December 1927 (Figures 2–5).

18 December 1927. The contrast between this pressure pattern and the mean pattern in Figure 1 is obvious. In place of an "Icelandic Low," a ridge of high pressure lies over Greenland, Iceland, and northwestern Europe; the highest pressure (1,040 millibars) is over Scandinavia. From this ridge of high pressure the gradient falls steeply to an elongated Low (980 millibars)

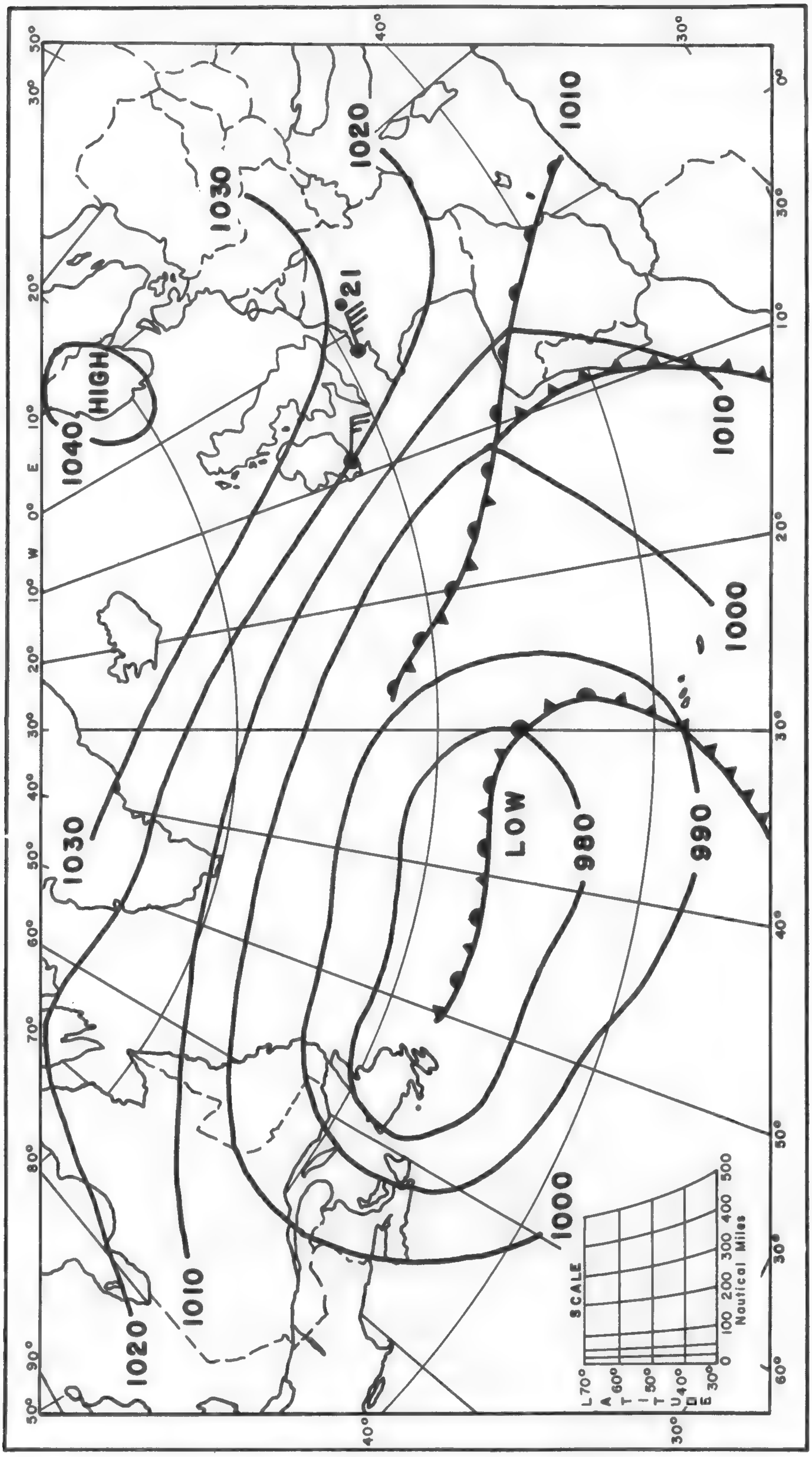

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Figure 2. The North Atlantic weather pattern, 1300 GMT on 18 December 1927. Note the ridge of high pressure over Greenland, Iceland, and Scandinavia, and the temperature of 21°F at Paris. The clockwise airflow around the High brought extremely cold air from the east into western Europe.

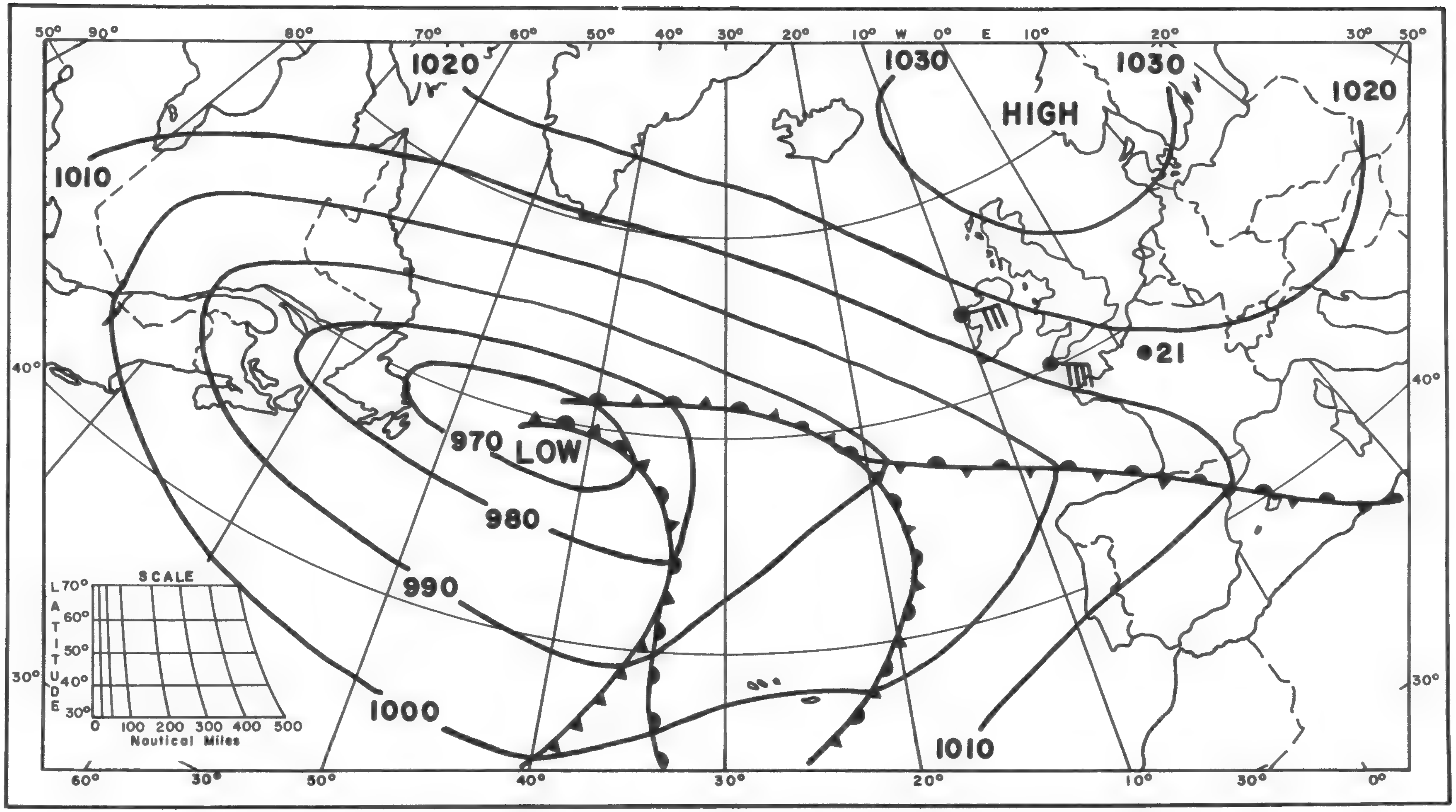
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Figure 3. The North Atlantic weather pattern, 1300 GMT on 19 December 1927, six hours before the estimated departure of the Lapwings. The High persists over Scandinavia. There is a strong east-to-west airflow from the west coast of Ireland toward Newfoundland and Labrador.

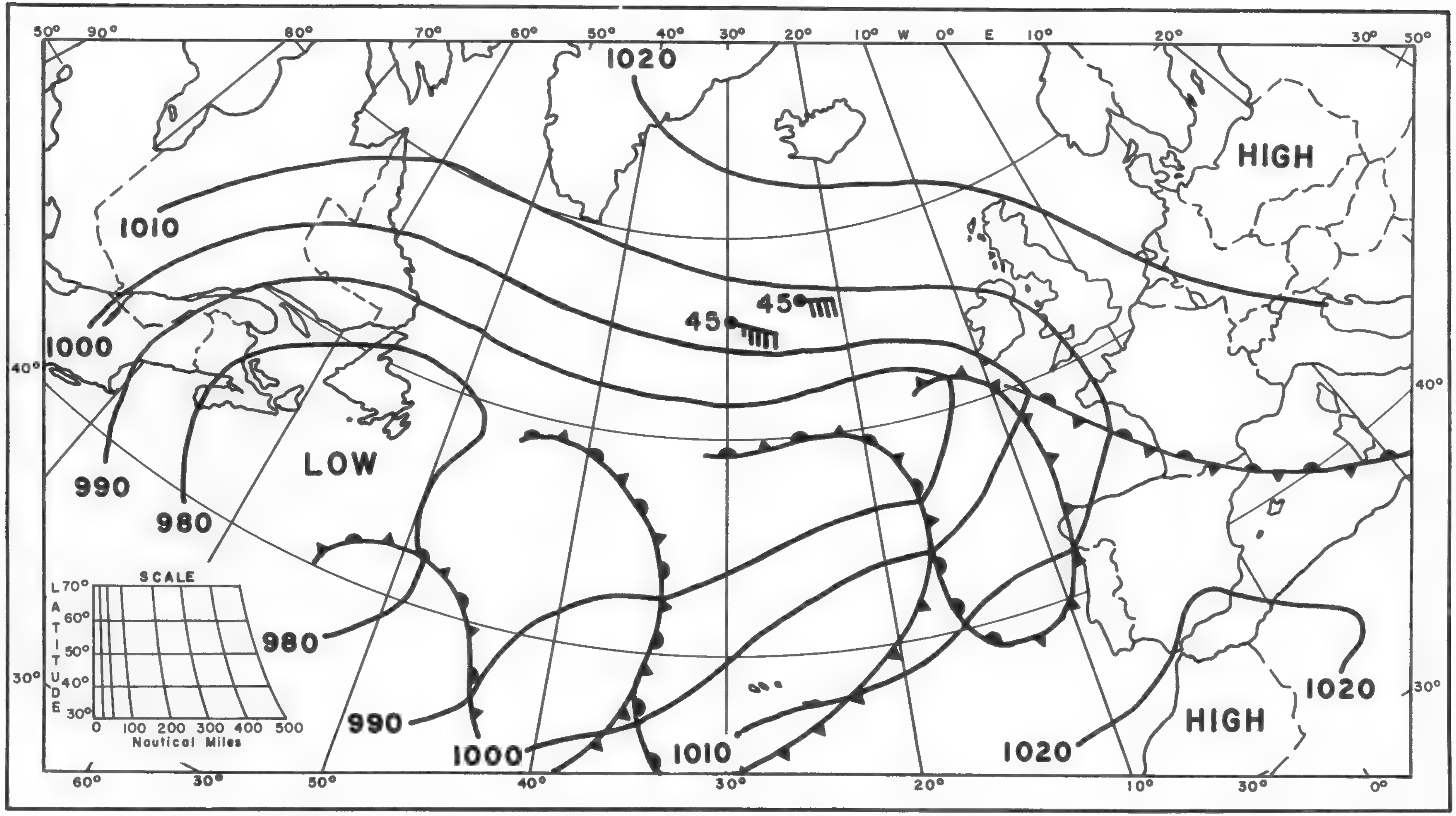
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Figure 4. The North Atlantic weather pattern, 1300 GMT on 20 December 1927. According to estimates, the Lapwings were over the North Atlantic where the winds were still strong from the east.

extending eastward from Newfoundland. The clockwise airflow around the Scandinavian High is bringing cold air from the *east* into western Europe. The temperatures at Amsterdam and Paris are, respectively, 18° and 21° F; since these are readings as of 1300 GMT (early afternoon), they probably are close to the high temperatures for the day. An east wind of about 35 mph is shown on the French coast. The *counter-clockwise* airflow around the Atlantic Low combines with the *clockwise* airflow on the southern side of the high pressure ridge to cause a strong east-to-west stream of air, flowing nearly parallel to the isobars, from western Europe towards Labrador.

19 December 1927. This map for 1300 GMT shows the pattern prevailing six hours before the 7:00 PM (1900 GMT) departure time which Witherby estimated for the Lapwings, on this date. The ridge of high pressure persists, extending from Ellesmere Island to northern Europe. The Low center east of Newfoundland has deepened to 970 millibars (28.65 inches). This is an intense and huge Atlantic storm, extending from eastern Canada to France and Spain. The 21-degree temperature at Paris shows that the cold persists in western Europe. The wind symbols show an east-southeast wind of about 43 mph at Land's End, England, and an east wind of about 28 mph on the west coast of Ireland. The trend of the isobars indicates a strong east-to-west airflow directed towards northern Newfoundland and Labrador.

20 December 1927. By Witherby's reckoning, the main numbers of Lapwings were over the North Atlantic at this time (1:00 PM, GMT; 9:00 AM, AST). The high pressure ridge to the north has weakened slightly, and the low pressure area is more diffuse. Of greatest significance, however, is the persistence of a steep pressure gradient within an east-west band over the North Atlantic, between the isobars for 990 and 1,010 millibars. We are fortunate to have two shipboard observations, made close to midocean and within this band. Both observations show the same air temperature: 45°. This reflects the extent to which the cold air from eastern Europe has become modified in its passage over the relatively warm waters of the eastern Atlantic. Moreover, this westward-flowing stream of mild air is streaming towards Labrador, which is relevant to the point made by Austin: that the Lapwings were arriving in Labrador "during a spell of exceedingly mild weather during the week before Christmas" 1927. Equally important are the midocean shipboard wind data: winds from the east, and ranging between 39 and 54 mph. Witherby cited evidence showing that the Lapwings' air speed (the speed of their flight in calm air) averages 45 mph. Therefore, in the present case, if they were flying westward within a westward-flowing airstream whose average velocity was about 45 mph, the birds' ground speed (i.e., their speed over the ocean) would be approximately 90 mph. Witherby pointed out, however, that the wind at 1,000 feet above the water must have averaged 55 mph from almost due east; if the Lapwings were flying at that level, their ground speed would be near 100 mph.

21 December 1927. The main numbers of Lapwings arrived in northeastern Newfoundland during 20-21 December. The important feature on this map for 9:00 AM, AST, on the 21st, is the persistence of a low pressure center (980 millibars) just off the southeastern extremity of Newfoundland. A fairly tight pressure gradient covers the area extending from this Low center northwestward over Newfoundland and much of the Labrador coast—the area within which most of the birds appeared. In analyzing the distribution of the Lapwings in eastern North America in this flight, we must "see" very clearly the *counter-clockwise* wind circulation around the Low center. For the recurving of the isobars, west of the Low center, shows that any Lapwings which failed to land in Labrador, Newfoundland, New Brunswick, and Nova Scotia would probably be carried southward and southeastward, and on over the Atlantic again.

As we saw, Austin reported that the Lapwings appeared along some 300 miles of the Labrador coast, as far north as Hopedale, during very mild weather in the week before Christmas. While no precise dates are available, the weather maps suggest strongly that the birds were arriving in Labrador sometime during 19-21 December 1927.

Witherby and Ingersoll provided quite explicit testimony for Newfoundland. Near the tip of Cape Bonavista, the birds first appeared on the afternoon of 20 December, in small groups of from 2–3 to 15–20 individuals. But on the morning of 21 December, one person saw an estimated 500 Lapwings there, and another man said that he saw 1,000 of these birds. Meanwhile, 150 miles to the northwest of Cape Bonavista, "hundreds" of Lapwings were seen at Harry's Harbour, Notre Dame Bay, "about" 20 December. Witherby also said that 50–60 Lapwings were present near Clarenville, about 60 miles southwest of Bonavista, during 20-23 December. Ingersoll reported that "flocks" of Lapwings appeared on 20 December in the Fogo District of Newfoundland, midway between Cape Bonavista and Notre Dame Bay. At Bonavista, according to Bent, one man killed 60 Lapwings; one of these, shot on 27 December, was the bird which had been banded in Cumberland, England.

While the main numbers of these birds made their landfall along the northeast coast of Newfoundland, others subsequently were found in various parts of that large island, and Witherby felt that there was indication of dispersal, especially southward and southwestward, from their center of arrival. Few were left at Bonavista at the end of December; the last was reported there on 15 January. Witherby also said that numbers of these birds perished around the shores of Fortune Bay, on the south coast of Newfoundland, at the end of December, but a good many still remained on nearby Burin Peninsula in the middle of February. Elsewhere, there is evidence that the airflow carried some Lapwings beyond Newfoundland. Witherby mentioned the occurrence of this species in Antigonish County, Nova Scotia, on 20 December. And the only Lapwing of the 1927 flight to be recorded in the United States was collected on 21 or 22 December in extreme northeastern Maine, a few miles from the New Brunswick line. This, again, demonstrates the fact that the weather pattern which brought the Lapwings to eastern Canada tended to divert, *away from* New England, any birds which did not land in Newfoundland or nearby areas of Canada. One Lapwing was collected in extreme eastern Quebec, near the Strait of Belle Isle. In the Canadian Maritime Provinces, a few were taken in New Brunswick, including the Grand Manan archipelago, while several were seen, and one was collected, in Nova Scotia.

1932: The Lapwing and the Dovekies

Dickens (1934) reported that, on 20 November 1932, she received a Lapwing which had been shot on Block Island, Rhode Island; from the context, we may judge that it was a fresh specimen. Miss Dickens also said that, on 16 November, she received a freshly dead Man-o'-war-bird (=Magnificent Frigate-bird, *Fregata magnificens*) which also had been shot on Block Island. Merrill Slate (pers. commun.) has informed me that these specimens are in the Block Island School collection, of which he is the curator.

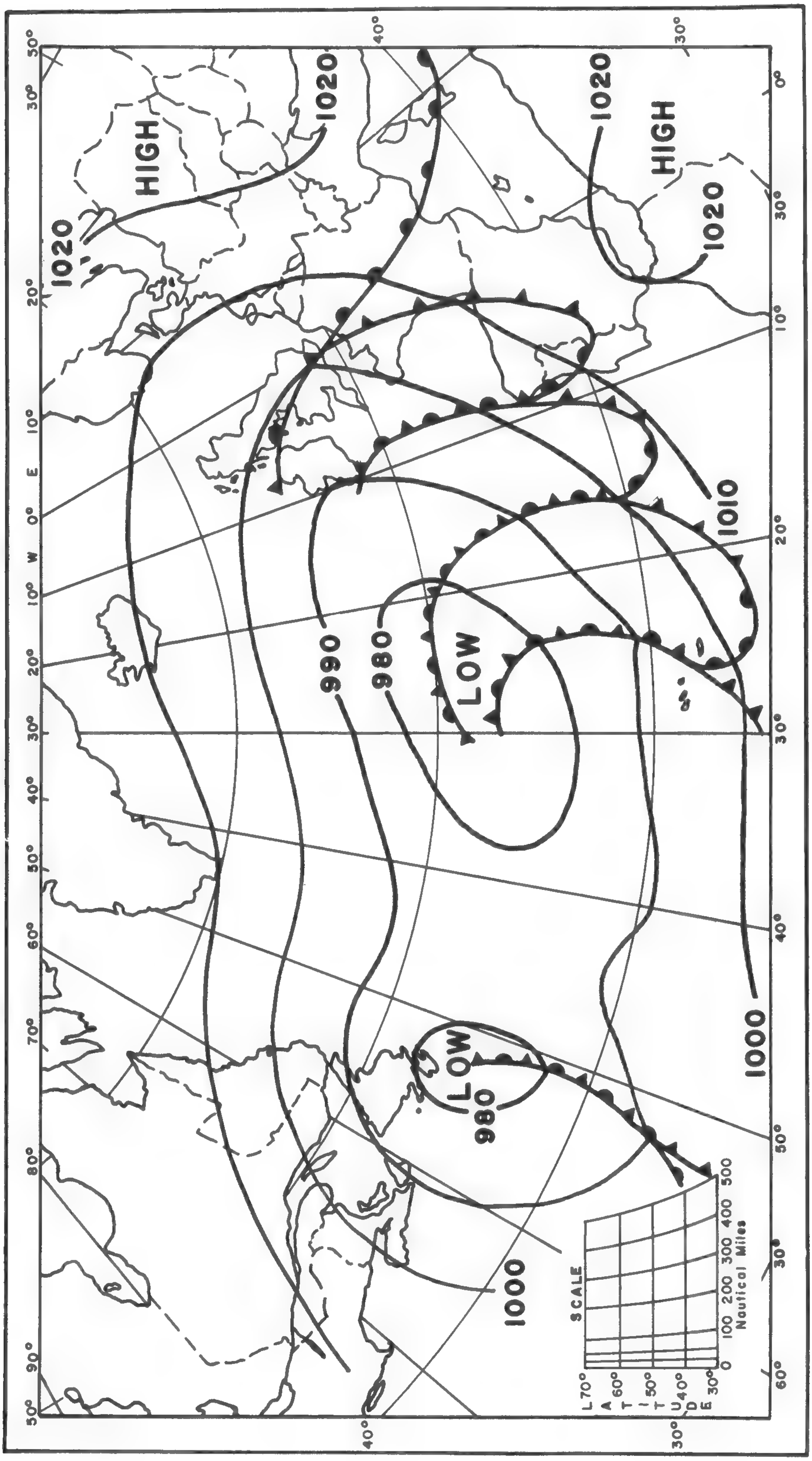
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Figure 5. The North Atlantic weather pattern, 1300 GMT on 21 December 1927. Note the Low off Newfoundland. The counterclockwise movement of air around this shows that any Lapwings which failed to land in eastern Canada on 20 or 21 December were probably carried south or southeastward and out over the Atlantic again.

The casual reader of Miss Dickens' note might not realize that the appearance of a Lapwing on Block Island, in the third week of November 1932, coincided with a remarkable phenomenon. That same month brought the most extensive influx of Dovekies (*Plautus alle*) ever recorded along the Atlantic coast from Canada to Florida (Murphy and Vogt, 1933). The latter paper quoted Miss Dickens to the effect that "it fairly rained Dovekies" on Block Island on, unfortunately, an unstated date in November 1932. But, from what Murphy and Vogt said about the manifestations of this Dovekie influx on nearby Long Island, New York, it seems likely that these alcids were present in numbers at Block Island during 19-20 November 1932, and that the Lapwing and the Dovekies appeared there simultaneously.

The North Atlantic weather charts for that month not only reveal why a series of weather situations caused so extensive an influx of Dovekies, but they also suggest why it was not too surprising that Block Island should receive, from widely separated regions, such species as the Magnificent Frigate-bird, the Lapwing, and the Dovekie within a few days. This will be the subject of another paper. The important point here is that this November 1932 record of the European Lapwing on Block Island lends some slight support to the suggestion, mentioned by Murphy and Vogt, that the successive influxes of Dovekies along the Atlantic coast in November 1932 may have included birds from Old World breeding grounds.

The 1966 Flight

In January 1966, at least 30 Lapwings appeared in eastern Canada and the French islands, St. Pierre et Miquelon, which lie 15 miles off the tip of the Burin Peninsula on Newfoundland's south coast (Christie and Emery, 1966). My first knowledge of this flight came from W. Austin Squires (pers. commun.) in late January, and I then corresponded with him and with several other Canadian ornithologists—Ford Alward, Charles Bartlett, Raymond Cayouette, David Christie, Phyllis Dobson, Anthony J. Erskine, W. Earl Godfrey, and Leslie and Mary Tuck. All had obtained pertinent information on the flight either directly or indirectly. Mrs. Tuck very kindly forwarded to me the reports which came in to the office of the Canadian Wildlife Service at St. John's, Newfoundland, including several Newfoundland records compiled by Harold Horwood and a copy of Michel Borotra's report on occurrences in St. Pierre et Miquelon. Table 2 presents all available North American records of the 1966 Lapwing flight.

A particular point of inquiry in the above-mentioned correspondence involved the exact date on which the Lapwing at St. Peters, Richmond County, Nova Scotia, was first observed. For the reported date, 10 January, was eight days earlier than the next firm date, 18 January, when the records began to concentrate chronologically. Nevertheless, very careful investigation confirmed the fact that the St. Peters bird—now in the private collection of John Lunn, Louisbourg, Nova Scotia—actually was first identified on 10 January. I was unable to find a good meteorological explanation for its presence in North America as of that date. But the record is valuable in suggesting, beyond reasonable doubt, that the January 1966 occurrences of the Lapwing in the New World cannot be attributed to one single 24-hour trans-Atlantic passage such as Witherby judged to be the case in the 1927 flight. However, we can relate the 1966 records to a mid-January cold spell in western Europe and to the Lapwings' response to the hard weather.

The accompanying 1966 weather maps show conditions prevailing at either 0000 or 1200 hours (midnight or noon) Greenwich Mean Time on certain dates in January. A time of 0000 hours for a given date marks the *beginning* of the day indicated. Thus, 0000 GMT, 15 January, represents midnight of the night of 14-15 January, on the meridian of Greenwich, England. To convert Greenwich Mean Time to Atlantic Standard Time, subtract 4 hours. Thus, 0000 GMT for a given date equals 2000 (8:00 PM) AST on the preceding date; 1200 GMT equals 0800 (8:00 AM) AST on the date given.

TABLE 2

The 1966 Flight of Lapwings

Date	*General area*	*Place*	*Number*	*Remarks*
10 January on	Nova Scotia	St. Peters, Richmond County	1	Died, early February; specimen
"mid-January"	Quebec Province	Manicouagan, Saguenay County	1	Killed by car; specimen
18 January	Newfoundland	Glovertown	1	Killed by car
18 January	Newfoundland	Deer Lake-Bonne	1	Picked up alive on Trans-Canada Highway
18-19 January	New Brunswick	Belledune, Gloucester County	1	
20 January	Nova Scotia	Mira Bay, Cape Breton County	2	One bird shot
21-29 January	New Brunswick	Red Head, St. John County	2	One bird present into February
22 January	Prince Edward Island	Black Pond, Kings County	1	At least one bird, possibly three
22 January	Newfoundland	Halls Bay Road	1	Specimen
23-24 January	Newfoundland	Conception Bay	3	
24 January	Newfoundland	Roberts Arm Road	1	
? January	Newfoundland	?	6	Reported in a flock
26 January	St. Pierre et Miquelon	Langlade Island	2	Specimen
26 January	St. Pierre Island		3	
27 January	Miquelon		4	Killed on or before 27 January; specimen
27 January	Newfoundland	Windsor	1	Hit a wire; specimen
2 February	St. Pierre		1	Seen flying
26 February	Nova Scotia	Halifax	1	Heard calling as it flew over

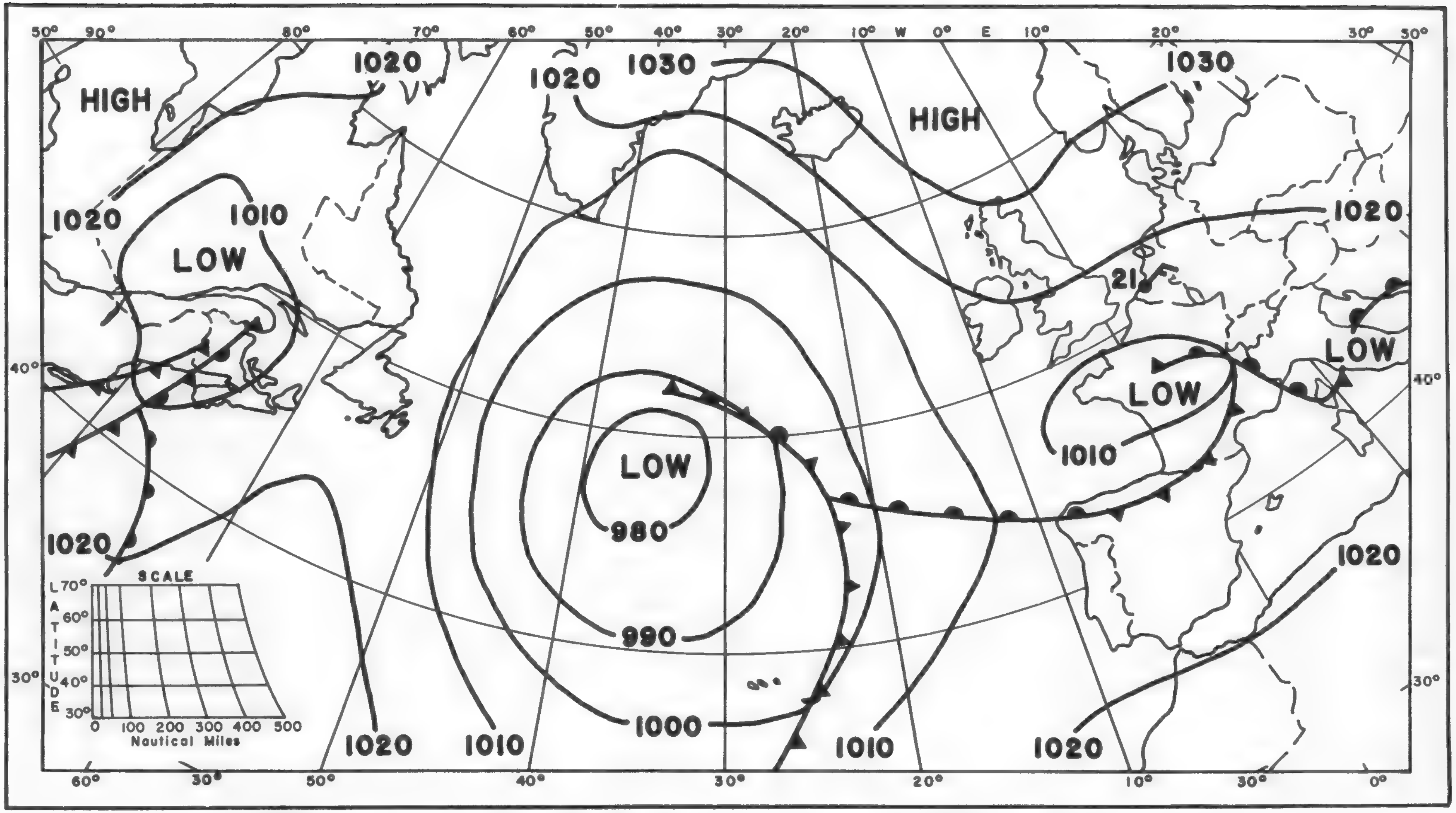
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Figure 6. The North Atlantic weather pattern, 1200 GMT on 11 January 1966. Note the High between Iceland and Scandinavia. Cold air from the east is pouring into the Low Countries and England. On 10 and 11 January observers noted a westward and southwestward movement of Lapwings in England.

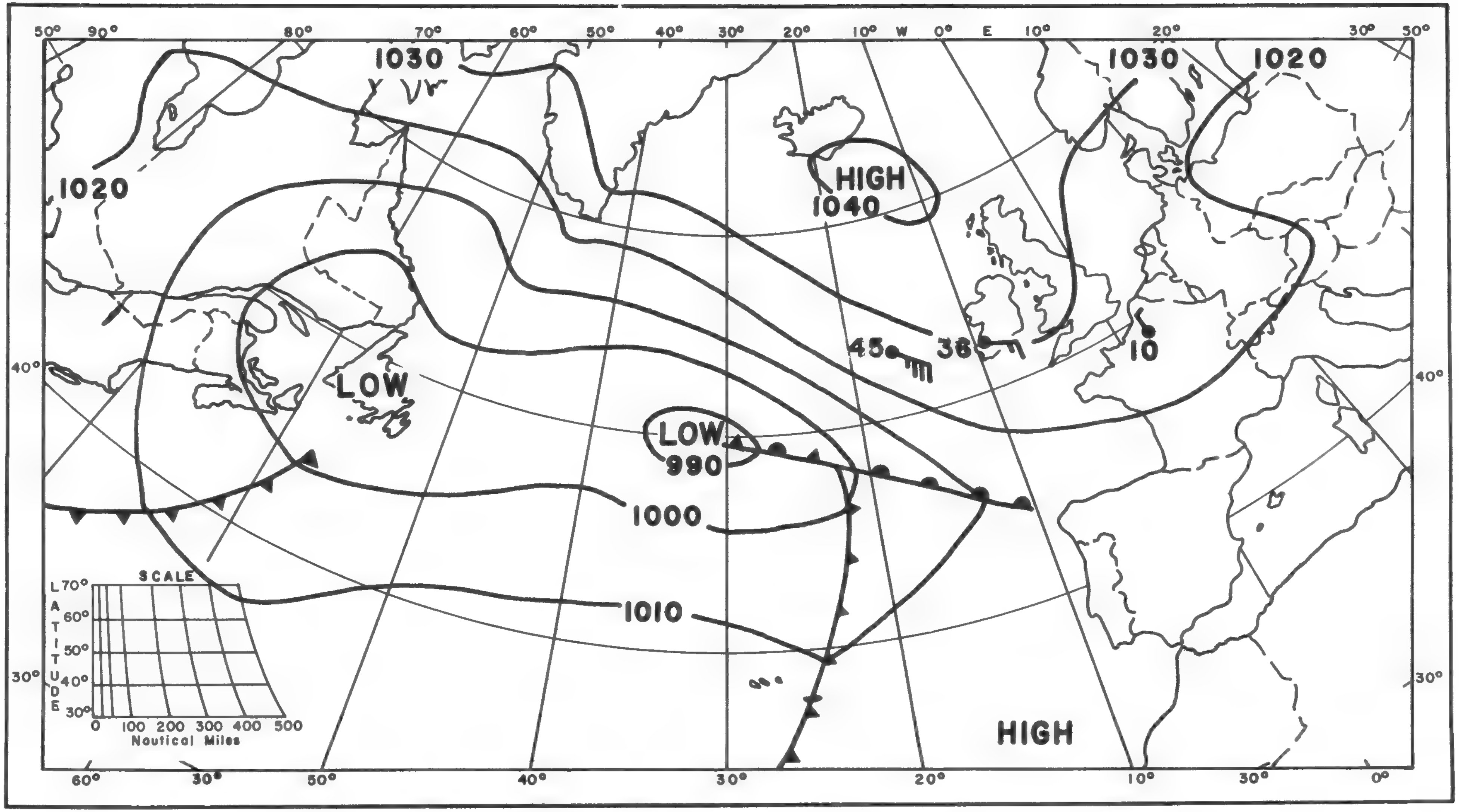
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Figure 7. The North Atlantic weather pattern, 0000 GMT on 15 January 1966. Note the High over Iceland, the low temperature at Paris, and east winds over western Ireland. This midnight pattern preceded the day that observers saw Lapwings stream over the Irish Sea into Ireland.

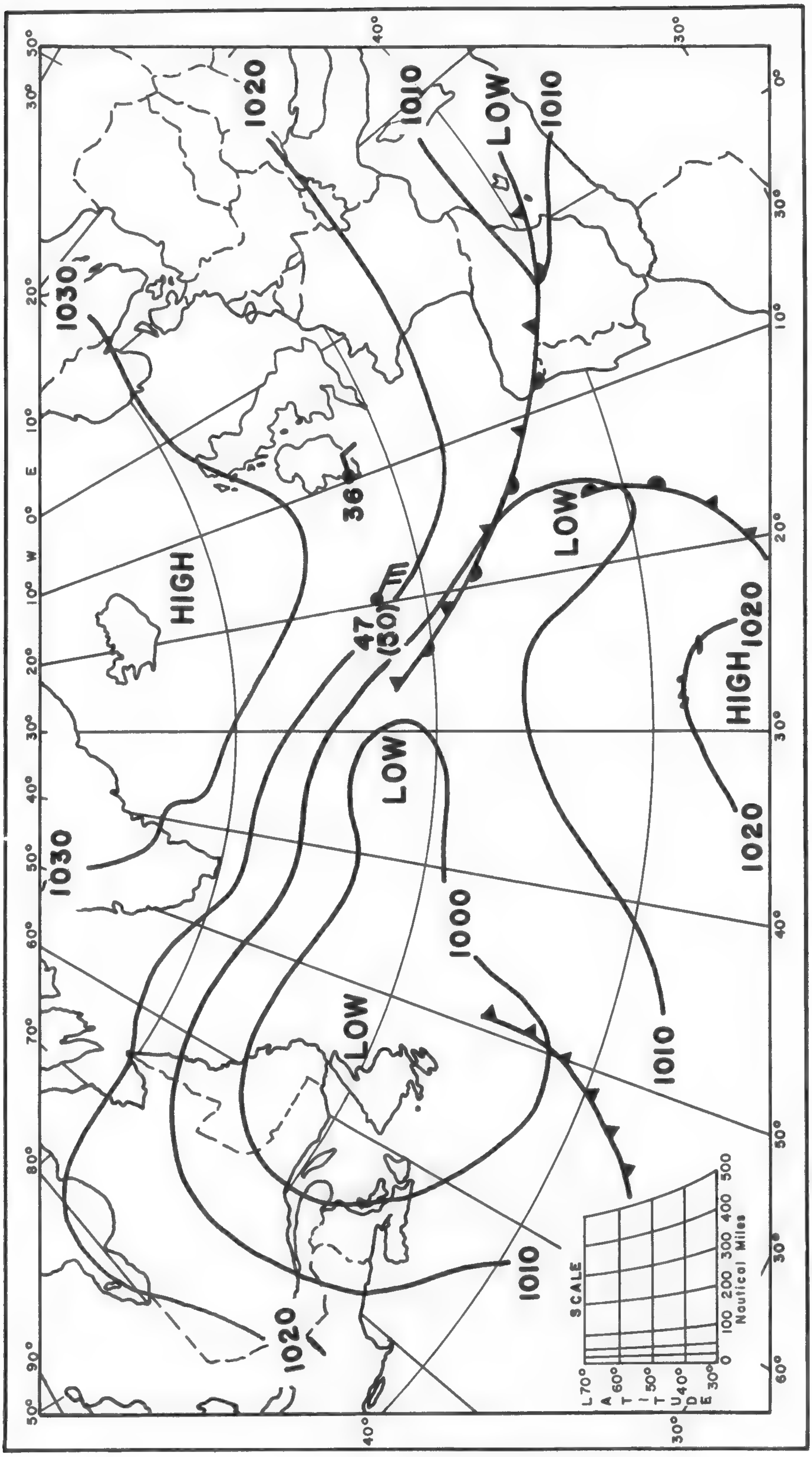
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Figure 8. The North Atlantic weather pattern, 1200 GMT on 15 January 1966. All day Lapwings flew into Ireland where the wind was east and cold. Note the east-west trough of low pressure from Spain to the Gulf of St. Lawrence.

The first map, for 1200 GMT (8:00 AM) on 11 January, shows cold air flowing from the east into the Low Countries and England. (Note the noontime temperature of 21° F, and the 15-knot northeast wind, at Brussels, Belgium.) Peter Davis (pers. commun.) wrote from England: "A considerable weather movement of Lapwings was observed with the onset of a spell of severe weather on the 10th-11th January. I have over a dozen records of westward or southwestward movement in central and southern England (Warwickshire, Oxfordshire, Nottinghamshire, Gloucestershire, and Sussex), involving several hundred birds on one or both of these days. From the Daily Bird Count reports [received by The British Trust for Ornithology] it is obvious that some movement of Lapwings to west and southwest continued in southern and central England each day [during the] 12th-17th (when the cold weather and easterly winds were still in force)."

On at least one date during 12-17 January, Lapwings were streaming westward over the Irish Sea and into Ireland. This was on 15 January. The maps for 0000 and 1200 GMT on the 15th (Figures 7 and 8) show the weather patterns which preceded and accompanied observations made that day in County Dublin, Ireland. An important feature of the map for midnight (GMT) of the night of 14-15 January is the area of high pressure over Greenland, Iceland, and northwestern Europe. (The fact that the highest pressure, 1,040 millibars, is near Iceland emphasizes the absence of an "Icelandic Low"!) A tight pressure gradient separates the northern High from an east-west trough of low pressure extending from just west of Spain to the Gulf of St. Lawrence. The 10° F temperature at Paris underscores the coldness of the air which has overrun western Europe.

R. F. Ruttledge (pers. commun.) wrote from Ireland: "A reliable observer, Oscar Merne, saw Lapwings coming in from the east, over the sea, in flocks of various sizes, fairly constantly all day of 15 January. He made his observations along the whole coastal sweep of Dublin Bay, from Dun Laoghaire to Sutton and Baldoyle. The birds were flying straight in from the east. A fair inference, therefore, is that they would have come from Anglesea, in northwest Wales. They were coming in all day, and the rate was about 600 per hour. By our standards, the weather had been *very* cold about 15 January." Ruttledge also mentioned a "cold southeast gale" on 19 January, and he felt that there was another influx of Lapwings into Ireland about 20 January.

We have no information to indicate precisely where or when the birds passed westward beyond Ireland and out over the Atlantic. If the Lapwings which reached North America included some which had crossed the Irish Sea from *northwestern* Wales (Anglesea), they may have overflown Ireland itself, perhaps at night. But if they were birds which flew westward from either the *southwestern* extremity of Wales (Pembroke), as Ingram and Salmon suggested they did in 1927, or the southwestern extremity of England (Land's End in Cornwall), they may have missed Ireland entirely. (For descriptions of hard-weather invasions of birds, including Lapwings, at Land's End, England, see Hudson, 1935.) Or, indeed, they could have been birds which had reached Ireland and had then resumed a westward hard-weather movement.

As for when the Lapwings became involved in the westward-flowing stream of air which carried them out over the Atlantic, we can only make estimates based on (1) the dates of their occurrences in North America, and (2) the testimony of the weather maps.

The "mid-January" record in Table 2 involves an adult male Lapwing which was killed by a car at Ruisseau Vert, near Manicouagan, Quebec Province, on the north shore of the St. Lawrence estuary; the specimen is in

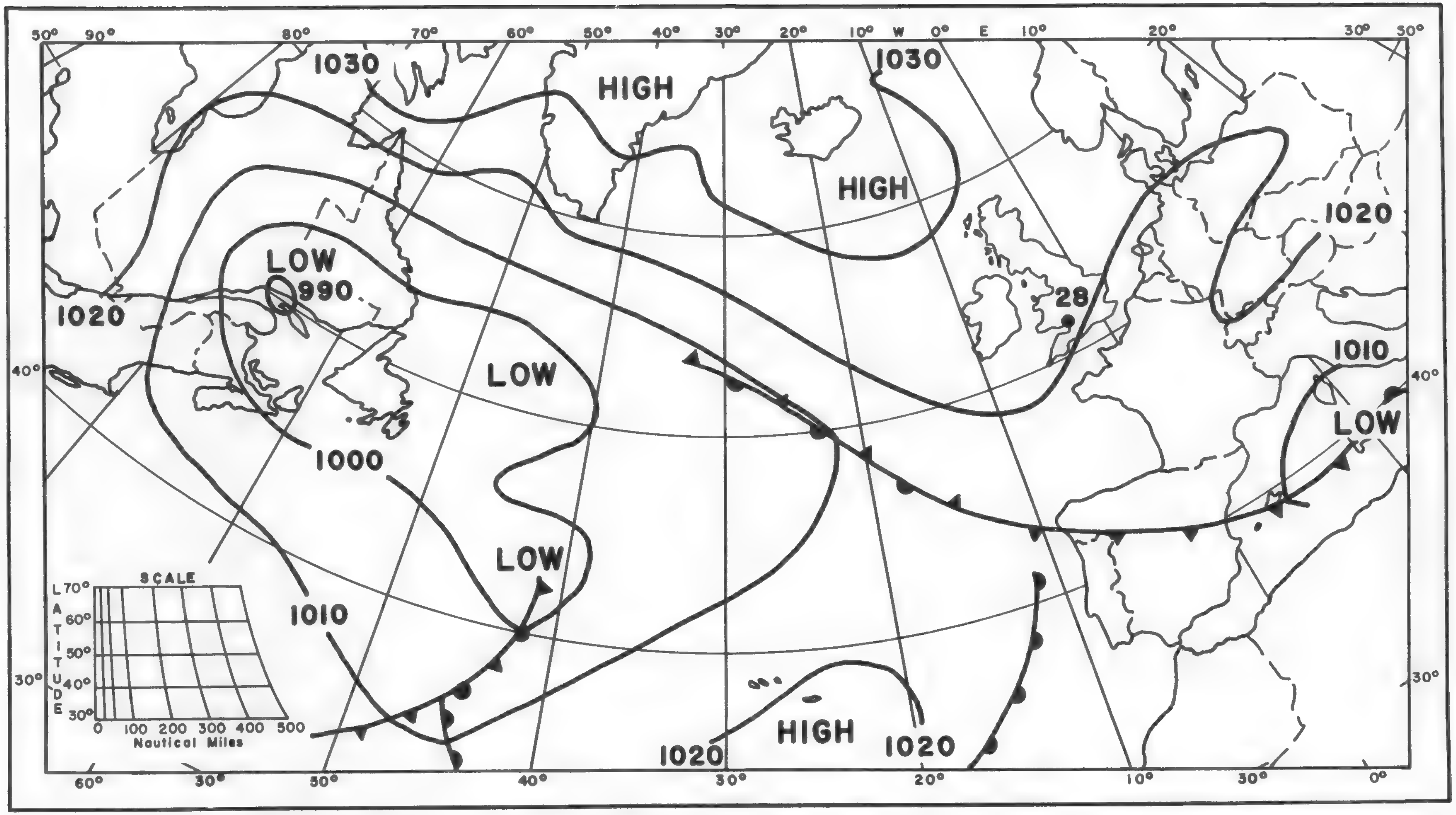
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Figure 9. The North Atlantic weather pattern, 0000 GMT on 16 January 1966. The low trough over the Atlantic continues.

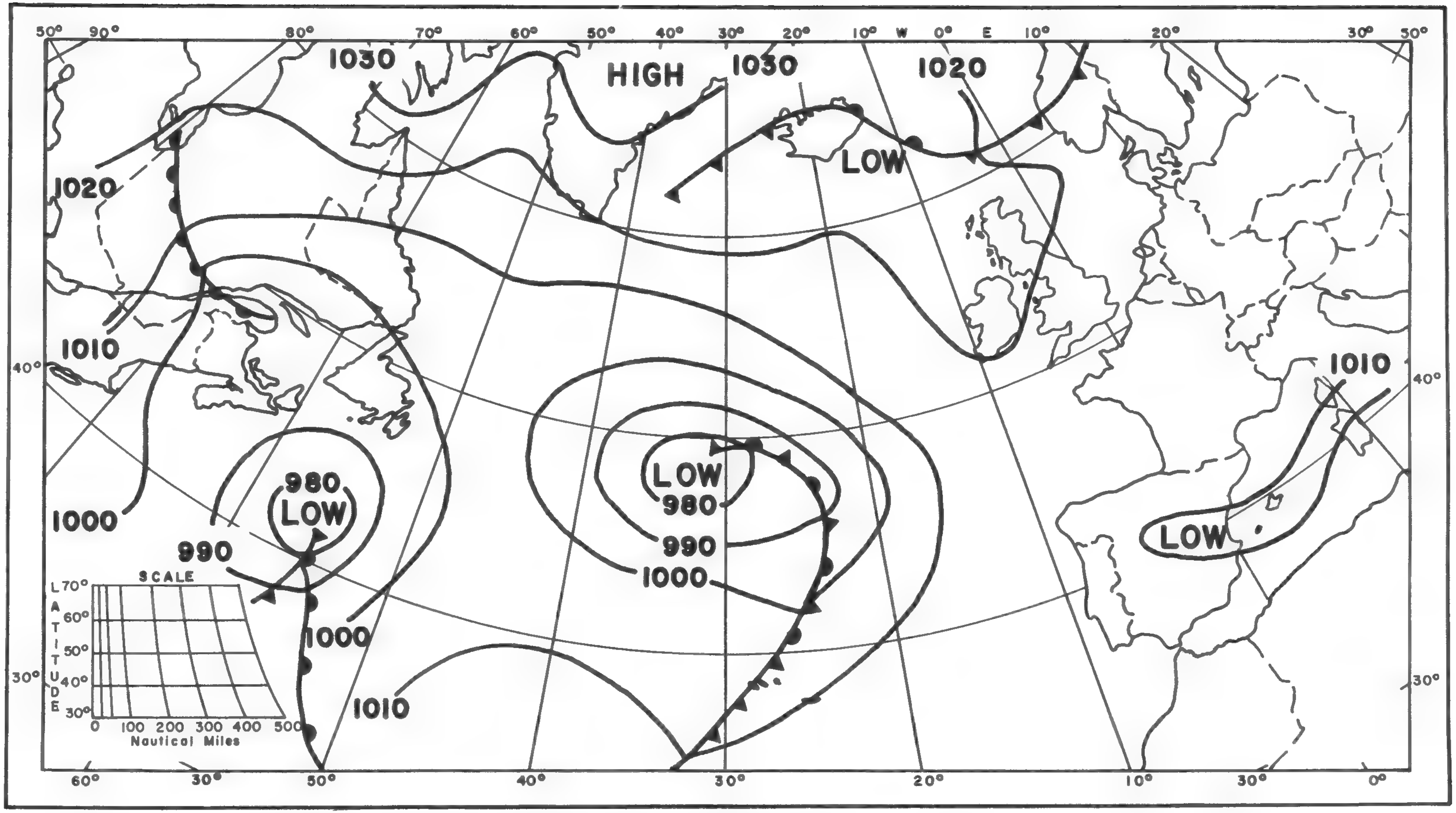
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Figure 10. The North Atlantic weather pattern, 0000 GMT on 17 January 1966. Note the warm front moving southwestward in Quebec Province.

the collection of the Quebec Wildlife Service (Raymond Cayouette, pers. commun.). The vagueness of the "mid-January" date for this record is unfortunate; for the purposes of analysis, it would have been helpful to know exactly when this bird was killed. Under the circumstances, we must base our analysis on the first three items in the series of records for which there are definite dates: those for 18 January.

At this point, it is a pleasure to quote the sound interpretations offered by Peter Davis, in England, and Finnur Gudmundsson, in Iceland. (In reading these interpretations, consult the maps shown in Figures 6–13, noting in particular the trends of the isobars, from day to day, across the North Atlantic.)

Mr. Davis (pers. commun.) wrote: "Looking at the weather maps for mid-January, I see that conditions were eminently suitable for westward 'drift' across the Atlantic for about a week from [the] 12th, though birds caught up in the easterlies during the first days of this spell would have been more likely to make a landfall in Labrador than further south; the ideal period so far as the [Canadian] Maritime Provinces are concerned would be [the] 17th-18th when the easterly airflow had shifted further south on your side of the Atlantic. The isobars are practically straight lines right across the ocean during the period, with a very steep pressure-gradient most of the time."

And Dr. Gudmundsson (pers. commun.) commented: "According to information received from the Meteorological Office in Reykjavik, the North Atlantic storm, which extended from Europe to [North] America [during] 17-19 January, did not touch Iceland; consequently it is not likely that drift migrants from Europe would have reached Iceland at that time, at least not to any extent." As we will recall, Dr. Gudmundsson reported that no Lapwing invasion occurred in Iceland during the winter of 1965-1966.

The maps for 15-16 January confirm Davis's suggestion that any Lapwings over the Atlantic at that time probably would have been drifted towards Labrador. So far, unfortunately, no Labrador records for 1966 have come to light. The low reading of 990 millibars over the St. Lawrence estuary, near Anticosti Island, at 0000 GMT on 16 January, prompts speculation that the bird killed near Manicouagan may have arrived there at about that time. The map for 17 January shows an unusual weather feature: a warm front moving *southwestward* in Quebec Province. This front marks the leading edge of mild air which has been modified in its westward passage over the relatively warm Atlantic waters, so that it is warmer than the cold Canadian air which it is displacing in Labrador and Quebec. This invasion of mild Atlantic air is reminiscent of the mention, by Austin, of the very mild spell in Labrador when the Lapwings were arriving there in December 1927. It seems likely that some Lapwings must have appeared there in January 1966.

When we come to the map for 0000 GMT on 18 January (8:00 PM, AST, on 17 January), we can shift from speculation to certainty that Lapwings were over the North Atlantic at this time, en route towards the Gulf of St. Lawrence area. Several features on this map deserve comment. The 10° and 12° F temperatures at Paris and Brussels, respectively, show that very cold weather continues in western Europe. By way of contrast, North Atlantic shipboard observations indicate air temperatures of 46° near midocean, 41° at a point east of Labrador, and 37° near the Strait of Belle Isle. More important, however, are the wind symbols at these three points: each symbol shows an east wind, and the velocities range from 35 to 45 knots (approximately 40–50 miles per hour). This strong airflow from the east is consistent with the steep pressure gradient between the Greenland High (1,030 millibars) and the Newfoundland Low (960 millibars). In this connection, there is a revealing similarity between the pressure patterns shown on the maps for 21 December 1927 and 18 January 1966; in each case, the significant feature is the Low center close to Newfoundland's Avalon Peninsula. The counter-clockwise wind circulation around the Newfoundland Low not only can be sensed from the curving of the isobars, but can be seen in the wind symbols at four shipboard observation points: *east* winds at the three points mentioned above, and a *west-northwest* wind (30 knots) at a point south of Nova Scotia.

This counter-clockwise wind circulation around the Newfoundland Low appears to be of critical importance in determining the area of eastern North America within which Lapwings might—and *did*—occur. For it is obvious that the airflow which carried the birds to Newfoundland, New Brunswick, Prince Edward Island, and Nova Scotia, would then carry southeastward and eastward any birds which had failed to land in the immediate vicinity of the Gulf of St. Lawrence. It follows from this that there is very small likelihood that Lapwings will reach New England in weather situations which can bring these birds to Newfoundland.

The maps for 18-20 January show that this same general pattern persisted for at least 48 hours—a huge ocean storm extending from eastern Canada to western Europe. I believe that the 1966 records for 18 January and following (Table 2) can be related to the persistence of this pattern during the 18th-20th.

A problem arises over the fact that the records for St. Pierre et Miquelon (15 miles off the tip of Newfoundland's Burin Peninsula) do not begin until 26 January. Did these birds reach North America several days after those which were recorded on the 18th and succeeding days? I feel that they arrived in Newfoundland sometime during 18-20 January, and that they subsequently moved southward onto and along the Burin Peninsula, and on to St. Pierre et Miquelon. It may be relevant that, in his account of the December 1927 flight, Witherby said that a good many Lapwings still remained on the Burin Peninsula in mid-February 1928. Witherby also said that, at the end of December 1927, numbers of these birds perished around the shores of Fortune Bay, which is immediately west of the Burin Peninsula, and which therefore is in the same general area as St. Pierre et Miquelon.

The final record in the early-1966 flight involved a Lapwing whose characteristic calls were heard—by an observer who had known the species in England—as the bird flew over Halifax, Nova Scotia, during a snowstorm on 26 February (Phyllis Dobson, pers. commun.). The record is interesting for its suggestion that this Lapwing probably had survived for at least a month somewhere in eastern Canada.

The Late-1966 Records

The presence of a Lapwing near Montauk Point, Long Island, New York, during 3-18 December 1966, will be reported by Thomas Davis and others in *The Kingbird.* This record deserves comment for at least two reasons. First, as I have mentioned above, the weather maps favor the possibility that the bird may have left Long Island on or soon after 18 December, flying southeastward in an airflow which could have directed it to Bermuda, where David B. Wingate saw a Lapwing on 26 December. In the second place, Montauk Point, at the eastern extremity of Long Island, is only 12 miles from Block Island, Rhode Island, and the December 1966 record brings to mind the Lapwing specimen obtained on Block Island in November 1932. A further coincidental point about the two records lies in the fact that the December 1966 Lapwing appeared on Montauk Point during or immediately after a

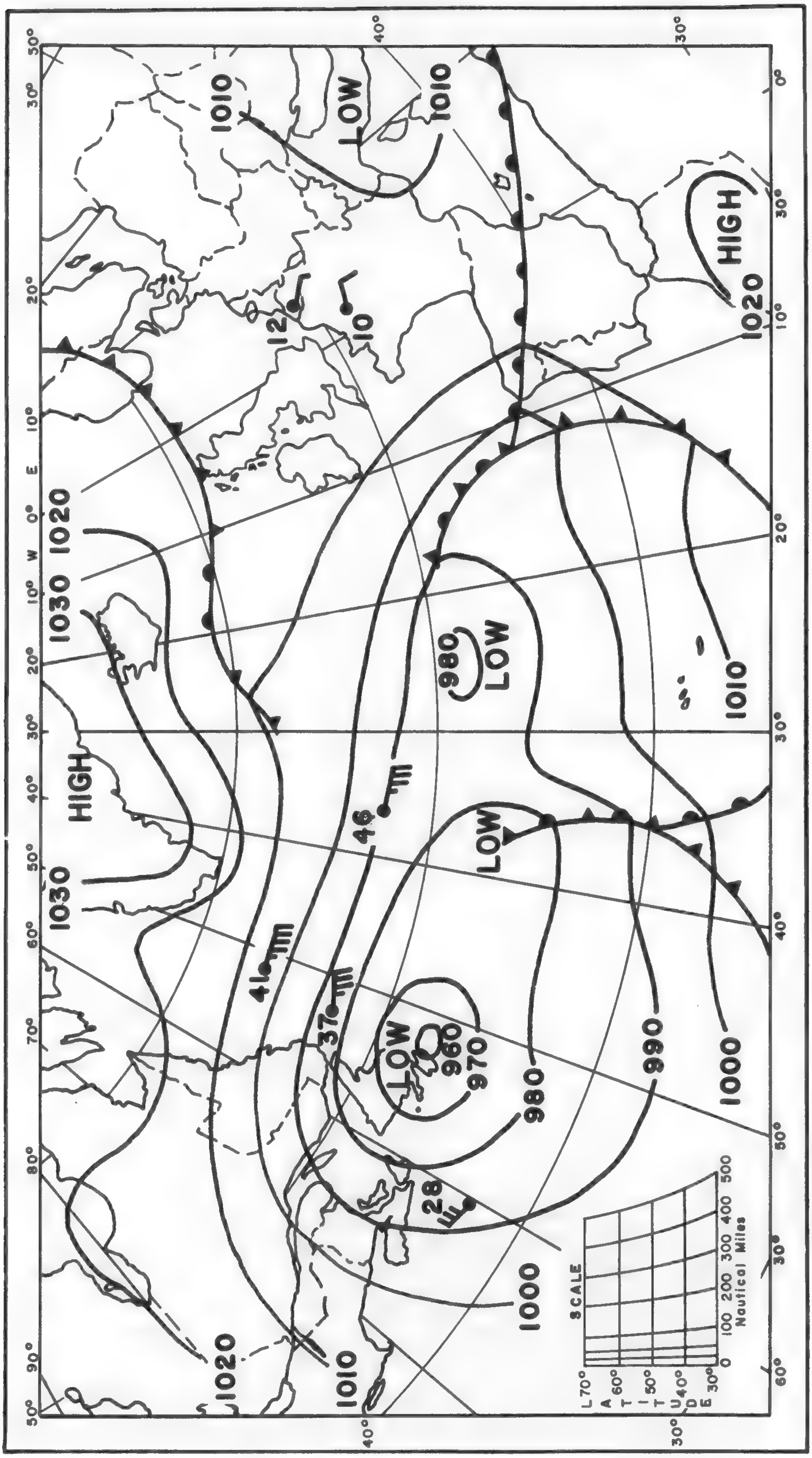
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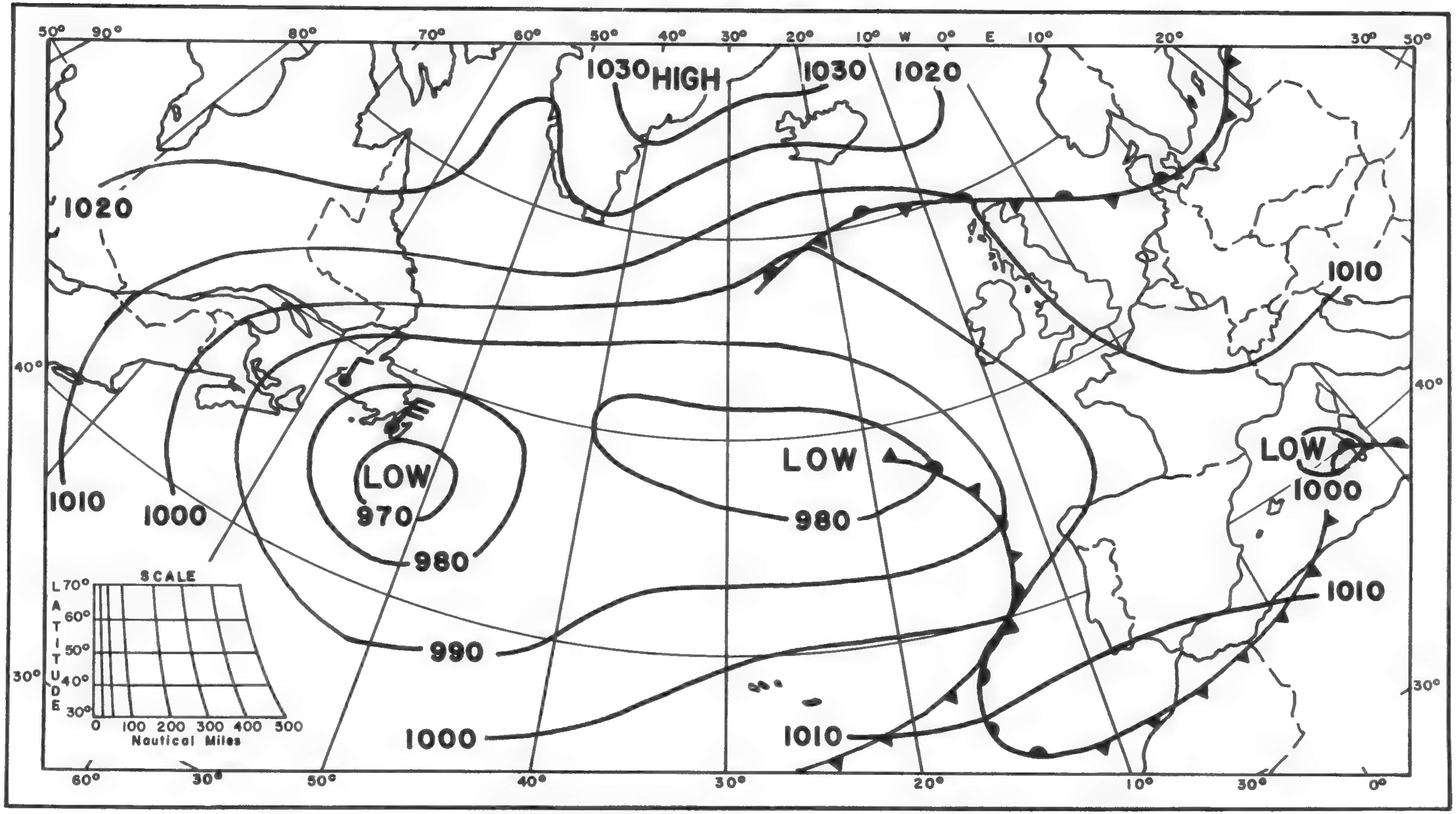
Figure 11. The North Atlantic weather pattern, 0000 GMT on 18 January 1966. Note the cold temperature at Paris and the much warmer temperature at sea. Because of the new Low, the winds are east and northeast off Labrador and west-northwest off Nova Scotia.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Nautical Miles
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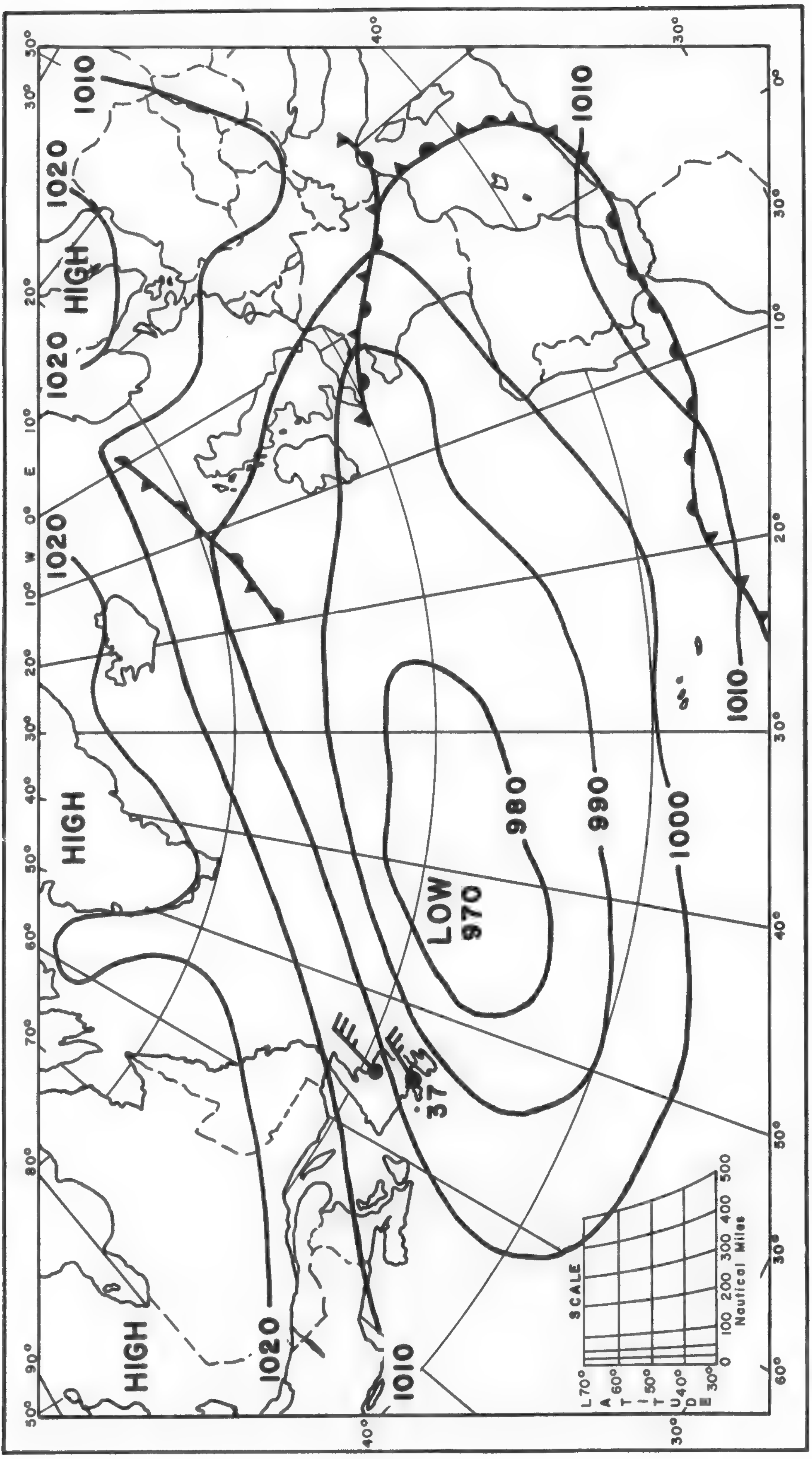
Figure 12. The North Atlantic weather pattern, 0000 GMT on 19 January 1966. The middle day of a huge storm extending from eastern Canada to western Europe.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100 200 300 400 500
Nautical Miles
10° W 0° E 10°

Figure 13. The North Atlantic weather pattern, 0000 GMT on 20 January 1966. The wind, northeast and strong over Newfoundland, tended to bring any birds to this coast and accounts for the records in Table 2. Lapwings missing the land would be blown out to sea again.

small but fairly extensive influx of Dovekies along coastal areas of Long Island and New Jersey (Thomas Davis, David A. Cutler, pers. communs.). Since the Block Island specimen of November 1932 was obtained during a great influx of Dovekies, we are presented with the possibility that meteorological correlations existed in the simultaneous occurrences of these two species, in November 1932 and December 1966, in that particular section of the Atlantic coast of the United States. However, when only one bird of a given species is represented in a stated situation, it is difficult, if not impossible, to arrive at a convincing meteorological explanation of its occurrence. The Montauk Point bird could have been a very recent arrival from Europe. But it also could have reached North America at the same time as the Lapwing which was shot on St. Pierre et Miquelon on 25 October 1966. This same difficulty applies to each of the isolated records in Table 1. Only in the cases of the flights of December 1927 and January 1966 was the volume of data sufficient to permit a reasonable degree of confidence in the meteorological interpretations.

Summary

The Lapwing (*Vanellus vanellus*) is a large Eurasian plover which has occurred accidentally in areas of the New World extending from Baffin Island to Barbados. This paper lists all known occurrences of the species in eastern North America, Bermuda, and the West Indies, during the period of 1883-1966. The available records tend to concentrate *seasonally* (November, December, January) and *geographically* (Newfoundland and the vicinity of the Gulf of St. Lawrence). There are only nine records for the United States; these records were obtained in the Atlantic coastal states extending from Maine to South Carolina. During the 84-year period for which North American records of the Lapwing exist, two particularly noteworthy flights have brought these birds to the vicinity of Newfoundland: (1) a remarkable invasion, involving hundreds of birds, in December 1927; (2) a much smaller flight in January 1966.

The main purpose of this paper is to examine these two flights in such detail as the available records, pertinent testimony, and meteorological evidence permit. A primary factor in the initiation of such flights is the response of wintering Lapwings to severely cold weather in western Europe.

The trans-Atlantic flights of this species in December 1927 and January 1966, and the pattern of the birds' occurrence in eastern North America on those occasions, appear to be the result of a particular series of events occurring in close sequence: (1) the irruption into western Europe of cold air from the east; (2) the resulting hard-weather movements of Lapwings westward into and within England and Wales towards Ireland; (3) the development of an anomalous weather pattern over the North Atlantic, in which a large, elongated Low extends from Europe to eastern Canada; (4) the involvement, in the vicinity of Ireland, of westward-moving Lapwings in the strong airstream flowing counter-clockwise around the Atlantic depression. This airstream directs the birds towards the Gulf of St. Lawrence area, but tends to divert seaward, away from the northeastern United States, Lapwings which do not land in eastern Canada.

On two occasions, a single Lapwing has been recorded in the area of Block Island, Rhode Island, and Montauk Point, New York, in conjunction with the inshore occurrence of Dovekies along that section of the Atlantic coast of the United States. The exact significance of this simultaneous occurrence of the two species is not evident. Similarly, isolated occurrences of the Lapwing in eastern North America cannot be interpreted meteorologically with any degree of confidence.

Acknowledgments

This paper represents the sum of the contributions of various persons whose assistance I gratefully acknowledge. In addition to those named above, in "The Lapwing's History in the New World," the following North Americans provided pertinent information or suggestions: Ford Alward, Charles Bartlett, Raymond Cayouette, David Christie, Roland C. Clement, Eugene Eisenmann, Anthony J. Erskine, C. Russell Mason, William B. Robertson, Jr., Merrill Slate, W. Austin Squires, Henry M. Stevenson, and Robert E. Woodruff. I am particularly indebted to Peter Davis, Finnur Gudmundsson, and R. F. Ruttledge for the revealing testimony which they sent from England, Iceland, and Ireland, respectively. And I am especially grateful to John H. Conover, of the Air Force Cambridge Research Laboratory, for his invaluable contributions, which include not only the weather maps accompanying this paper, but also professional advice on various meteorological matters. Mr. Conover based the 1927 maps on material in the U.S. Weather Bureau's Historical Northern Hemisphere Weather Maps; and the 1966 maps on data disseminated by the National Meteorological Center, U.S. Weather Bureau, ESSA, Washington, D.C. I also acknowledge most gratefully the kindness of: the McGraw-Hill Book Company for permission to adapt an illustration showing the "Mean Surface Barometric Pressure Pattern for January over the North Atlantic," from "Climatology" (1944) by B. Haurwitz and J. Austin; the Princeton University Press for permission to make brief quotations, and to adapt certain temperature data, from "Weather Around the World" (1943), by Ivan R. Tannehill.

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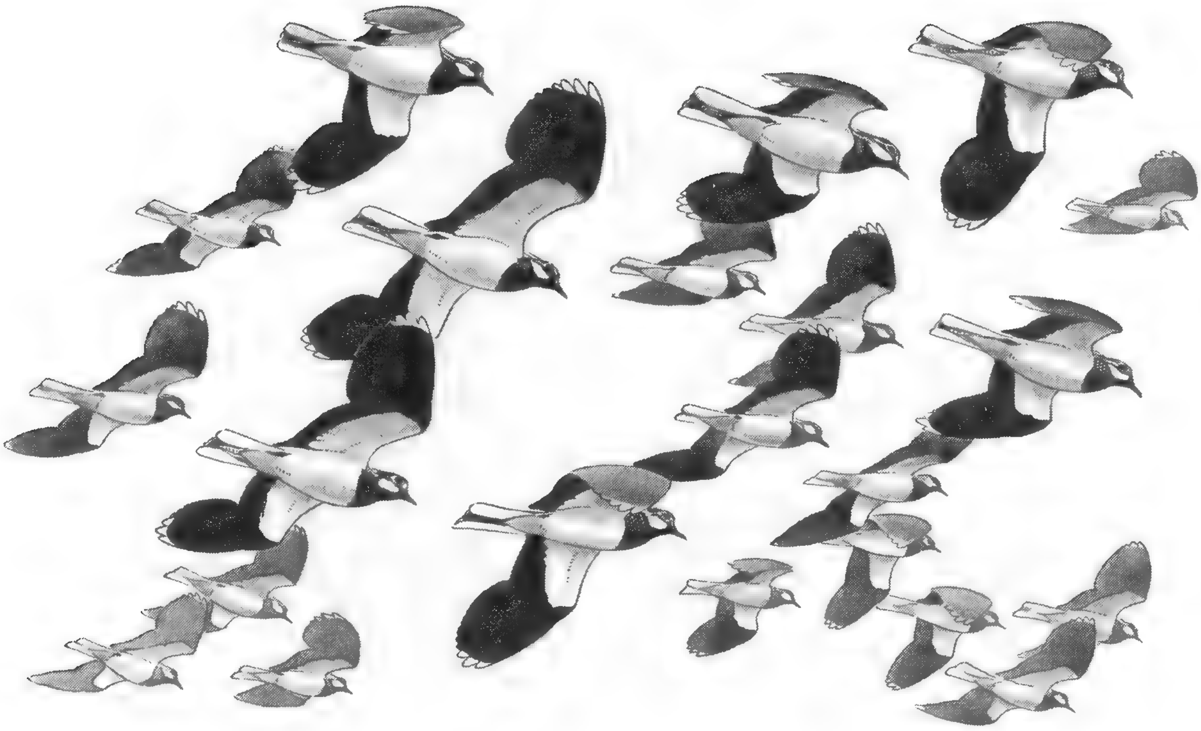


Lapwings. Drawing by Robert Gillmor.

THE DICKCISSEL ON ITS WINTERING GROUNDS IN TRINIDAD

Richard P. ffrench

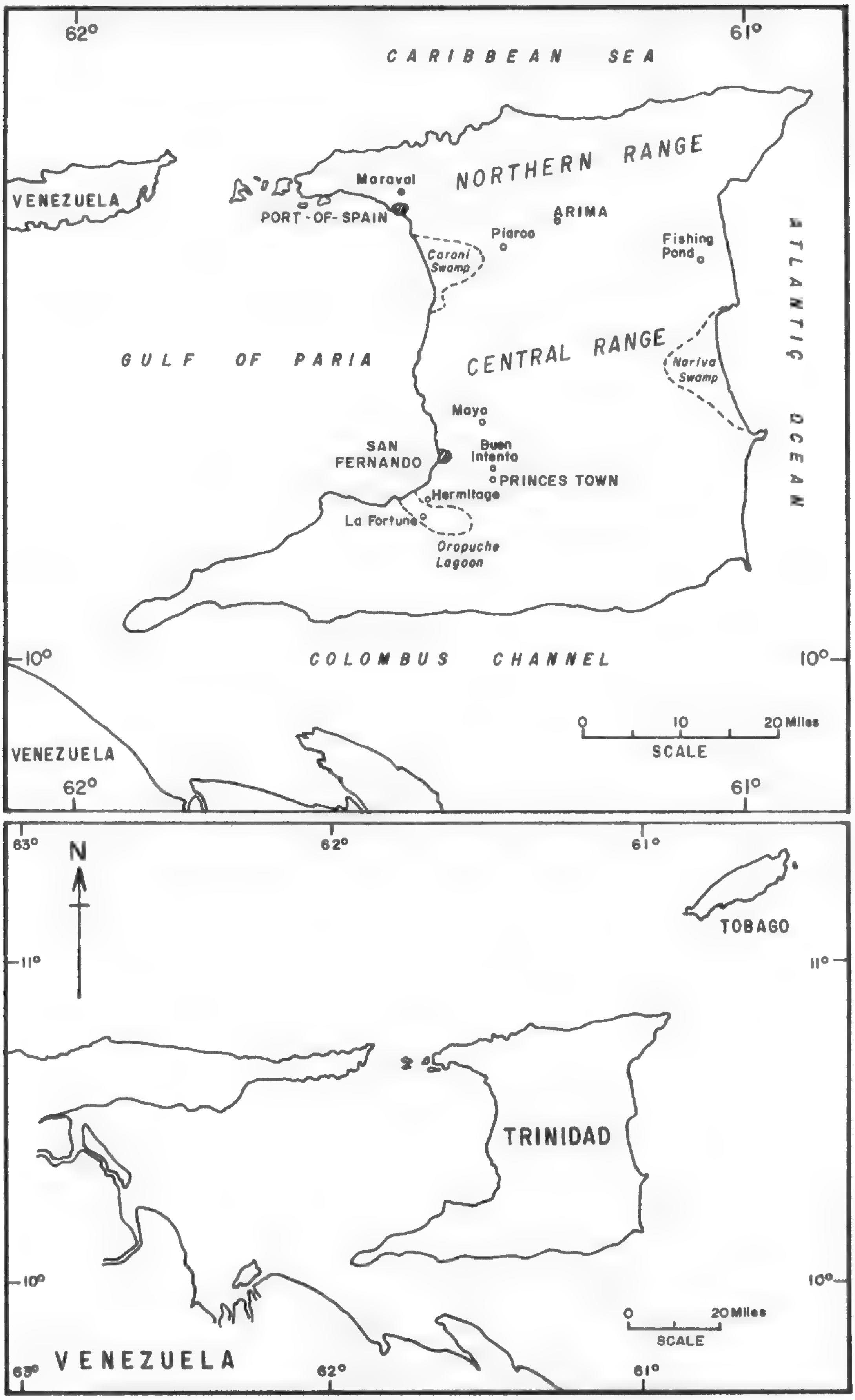
The Dickcissel (*Spiza americana*) shows an erratic distribution and remarkable fluctuation in numbers throughout its breeding range in North America and has aroused recent comment by turning up in great numbers during the winter in eastern United States (Gross, 1956). Many have been reported at feeding stations. Possibly the increase in the number of records may be due, at least partly, to the increase in feeding stations where the birds may be seen and to the growing throng of persons watching birds and reporting observations.

The Dickcissel normally winters from Mexico south through Central America to Colombia, Venezuela, Trinidad, and the Guianas. This paper concerns the Dickcissel wintering in Trinidad where, from January 1959 through April 1966, I trapped and banded 2,888 birds and made detailed observations on roosting, feeding, and daytime behavior. I also studied several birds confined in an outdoor aviary during the winter of 1964 and one pair which I kept from 1964 to 1966.

Status, Past and Present

Dickcissels winter commonly in Colombia and Venezuela (Phelps and Phelps, 1963). Records from Guyana and French Guiana are more casual and ornithologists working recently in Guyana and Surinam have not reported Dickcissels in any numbers. One specimen, collected at the Abary River in Guyana in July 1906 (Hellmayr, 1906) seems to be the only evidence for the bird's occurrence so far south on the eastern side of the continent. A specimen from Ecuador, in the collection of the American Museum of Natural History, constitutes the southernmost record on the western side.

The reports for the past hundred years indicate that the occurrence of the Dickcissel in Trinidad (Figure 1) has been variable: Leotaud (1866:316) stated that its visits were irregular; Chapman (1894) and André (see Hellmayr, 1906), who collected in Trinidad at the end of the nineteenth century, did not mention the Dickcissel; neither did Belcher and Smooker (1937), who worked during the third and fourth decades of this century. Although Junge and Mees (1958:134) included the Dickcissel in their check-list, Mees, who collected widely from August 1953 through February 1954, never saw a single bird.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CARIBBEAN SEA
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NORTHERN RANGE
PORT-OF-SPAIN
ARIMA
Piarco
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ATLANTIC OCEAN
GULF OF PARIA
CENTRAL RANGE
Nariva Swamp
Mayo
SAN FERNANDO
Buen Intento
PRINCES TOWN
Hermitage
La Fortune
Oropuche Lagoon
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11°
TRINIDAD
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20 Miles
SCALE
63°
VENEZUELA
62°
61°

Figure 1. Maps of Trinidad showing (*above*) the roosting and feeding areas occupied by Dickcissels during the winter season from January 1949 to April 1966 and (*below*) the relation of Trinidad to the northern coast of South America and the neighboring island of Tobago.

Recently the reports have been different: Smooker (pers. commun.) did observe Dickcissels in his later years—before 1950; a local newspaper (March 1951) mentions large numbers in the southern part of the island; Herklots (1961:266) observed large flocks in central and southern Trinidad in 1957; D. W. Snow (pers. commun.) saw a flock of 500 birds in eastern Trinidad in early 1958. Since my arrival in 1958, Dickcissels have been present regularly in southern Trinidad in very large numbers during the first four months of the year.

It is possible that the Dickcissel has been present every winter for many years in southern Trinidad and escaped notice because most of the ornithologists worked in the northern part of the island. Evidence from local farmers, rarely reliable, is conflicting. Some state that the bird has always been present in winter; others insist that it has been present only in recent years. Since, as I shall show, the Dickcissel is extremely conspicuous in its wintering grounds and could not have been overlooked, I feel that the bird is as erratic in its distribution at the extreme limit of its winter range as it is on its breeding range.

Annual Occurrence of the Dickcissel in Trinidad since 1959

Dickcissels begin to arrive in Trinidad in December and achieve their full numbers in January (see Figure 2). Their arrival is considerably later than the other regular North American migrants of which the majority—the shorebirds, ducks, and warblers—arrive any time after mid-August with very few individuals appearing to be in passage after early-November. Since a maximum coverage was not possible every year, the earliest records given in Figure 2 are in those years when I made a determined effort to record the first arrivals.

Bond (1960:240) records Dickcissels only in the western islands of the Caribbean from Jamaica westward. We have no records from Tobago, Grenada, or any of the Lesser Antilles. Clearly, the Dickcissel's route to and from Trinidad is from the west by way of Venezuela where the bird is regularly recorded from November through April with some individuals remaining until June (Phelps and Phelps, 1963; Friedmann and Smith, 1955). Paul Schwartz (pers. commun.) reports that they arrive in Venezuela in great numbers at the end of September and early October. In Venezuela, the llanos become very dry by late December and it may be that this drought forces the Dickcissels to move on. In Trinidad the dry season usually does not begin until January and is never as extreme as in Venezuela. Actually the birds leave Trinidad in April before the driest conditions prevail.

If the drought is the cause of the Dickcissel's move east from Venezuela to Trinidad, it is not surprising that the date of arrival of most Dickcissels in Trinidad can vary by almost a month—from mid-December to mid-January. In contrast, the spring departure of the majority of these birds takes place within one week of 16 April. I have watched the Dickcissels depart on a number of occasions and in every case the direction of their flight has been due west toward Venezuela. This westward movement corresponds with the April records in Venezuela.

Distribution, Habitat, and Feeding

The Dickcissels in Trinidad can often be separated neatly into three populations, each of which feeds and roosts in one or two particular areas: (1) The population, which feeds in the Oropouche Lagoon and the low hills

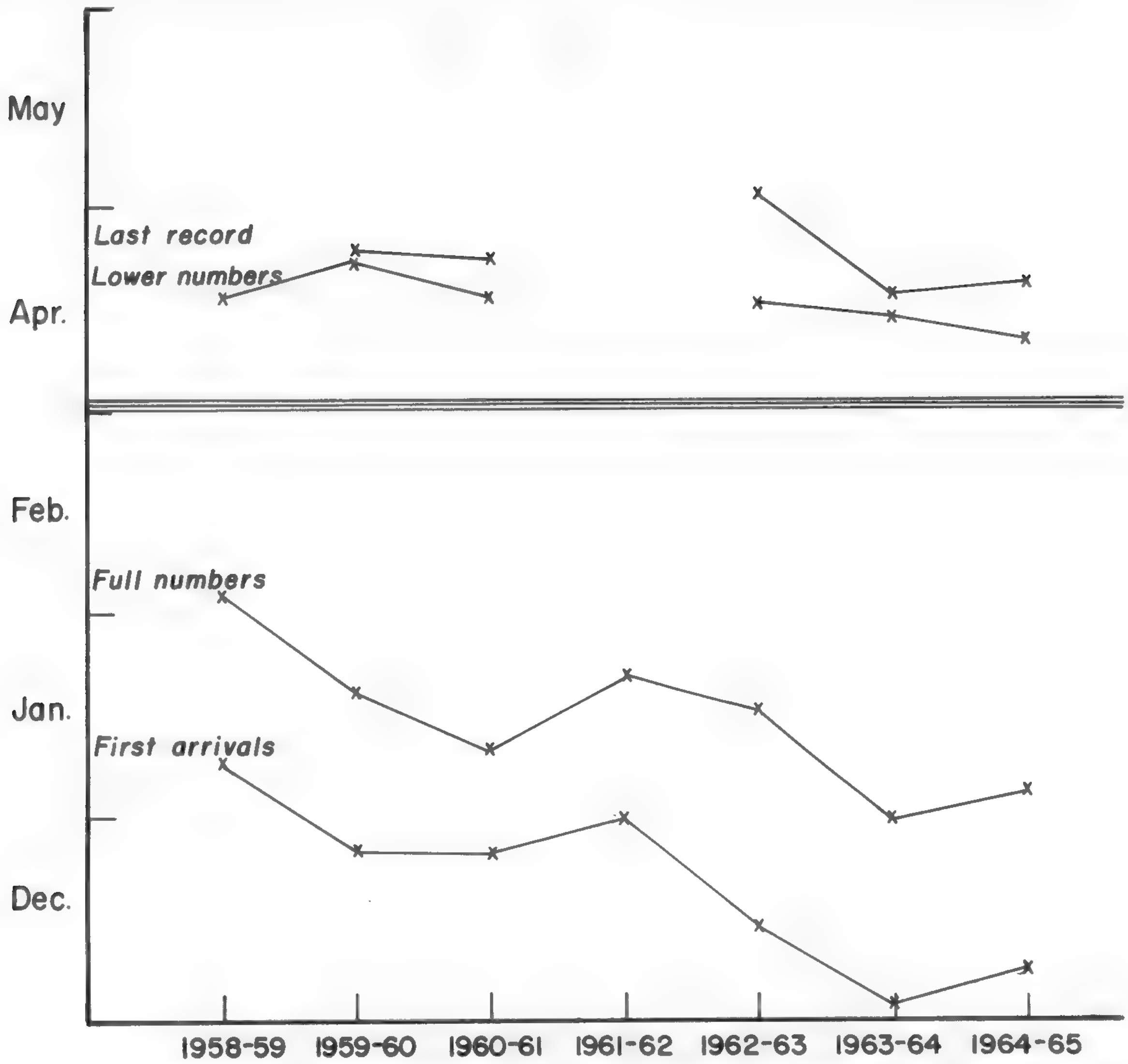


Figure 2. The dates of arrival and departure of Dickcissels in Trinidad. The first birds almost always appeared in December and all were there by January. In the spring most of the birds left within one week of 16 April and usually all were gone by 1 May.

around Princes Town and Mayo and roosts either on the edge of the lagoon at La Fortune, Hermitage, or Debe or at Buen Intento some 15 miles distant (see Figure 1); (2) the population which feeds in the Caroni marshes and in the foothills and valleys of the Northern Range and roosts near Piarco; and (3) the population which feeds in the Fishing Pond and Nariva Swamp and roosts on the edge of the swamp. I was principally concerned with the population at the Oropouche Lagoon.

Rice, which seems to be the Dickcissels' chief food, is grown in these three areas. Fortunately for the farmers, the Dickcissels arrive immediately following the rice harvest in November and depart before the harvest in June. The birds apparently feed on the rice left in the fields. I have seen flocks of Dickcissels congregate about the stacks of rice straw, which the farmers collect, picking up the grains on the ground. In the Nariva area the Dickcissels may benefit from the sporadic farming of some peasants who plant rice to ripen in both November and February, and after reaping the first and main crop frequently move on, leaving the second unharvested anyway.

W. H. Phelps (pers. commun.) stated that until the Venezuelan farmers learned to plant rice so that it would not ripen when the Dickcissels were present, the birds ruined many rice crops.

According to Paul Schwartz (pers. commun.), Dickcissels feed on the seeds of wild grasses in the Venezuelan llanos. This is true in Trinidad as well, especially in the more hilly districts where there is no rice. Foraging parties have been seen as high as 500 feet above sea level in various valleys of the Northern Range from Maraval to Arima. In the Mayo district the birds feed on the cultivated lands and in the scrub, concentrating on the wild grasses and leaving untouched the crops of maize (*Zea mays*), pigeon peas (*Cajanus cajan*), tomatoes (*Lycopersicum esculentum*), and ochroes (*Hibiscus esculentus*). They also avoid wooded areas and plantations of cocoa, citrus, and banana. The farmers have been unanimous in saying that the Dickcissel does not bother their crops.

In the Oropouche Lagoon, I observed the behavior of Dickcissels during the daytime in late February. On leaving the roosts in the early morning they flew in flocks to the feeding grounds and then immediately scattered. During the first hour they concentrated on feeding, frequently giving the normal single-note call, a grating *bjjt*. As the morning advanced, the birds tended to congregate more in flocks of up to 200; occasionally in a large flock of several thousands.

Dickcissels invariably frequented the cultivated lands, grassy pastures, ditches, bamboo clumps, and rough scrub. They never went into mangroves or reed beds, or anywhere distant from cultivation. On the other hand, during the daytime, they never entered the fields of sugarcane that bordered the lagoon.

When not feeding they formed groups, perching in tall weeds or maize, or in bushes or trees. Whenever a sizable group collected, there was considerable chirping, mostly an incisive *chick* or *jeep*, occasionally a song phrase *dick-dick-dickcissel* from a male.

No distinct associations were formed with any other species. The usual savanna birds were all present, including the Plain-breasted Ground-Dove (*Columbigallina minuta*), the Ruddy Ground-Dove (*C. talpacoti*), Smooth-billed Ani (*Crotophaga ani*), the Shiny Cowbird (*Molothrus bonariensis*), the Carib Grackle (*Quiscalus lugubris*), the Yellow-hooded Blackbird (*Agelaius icterocephalus*), the Red-breasted Blackbird (*Leistes militaris*), and the Ruddy-breasted Seedeater (*Sporophila minuta*). Other birds present in the area in smaller numbers were the Cattle Egret (*Bubulcus ibis*), the Striped Cuckoo (*Tapera naevia*), the Yellow-throated Spinetail (*Certhiaxis cinnamomea*), the Pied Water Tyrant (*Fluvicola pica*), the Fork-tailed Flycatcher (*Muscivora tyrannus*), and the Barn Swallow (*Hirundo rustica*).

On a hillside bordering the lagoon Dickcissels were perching and singing in the trees, mainly the smaller ones, but also in the mahogany (*Swietenia macrophylla*) and palms of various species. Here the bird fauna included the Barred Antshrike (*Thamnophilus doliatus*), the Great Kiskadee (*Pitangus sulphuratus*), the Yellow-bellied Elaenia (*Elaenia flavogaster*), the Gray-breasted Martin (*Progne chalybea*), the House Wren (*Troglodytes aedon*), the Rufous-browed Peppershrike (*Cyclarhis gujanensis*), the Grayish Saltator (*Saltator coerulescens*), and the Blue-black Grassquit (*Volatinia jacarina*).

At no time did I find any evidence of a particular association or competition with any of these species, most of which are resident in Trinidad.

I have no evidence that a pair bond was being formed between any of the Dickcissels in Trinidad. The distribution of the sexes appeared to be quite haphazard. The adult pair, held in the outdoor aviary from the early months of 1964 to January 1966, did show signs of breeding behavior in the summer of 1965 and attempted to build a nest.

Roosting Sites and Behavior

The Dickcissels roosted in sugarcane or in bamboo. The roosts I studied were in sugarcane fields where, with mist nets, I could always catch some, often many, birds.

Since the birds feeding in a certain area almost invariably congregated at one roost, it was possible to estimate the number of birds involved. After practicing with small flocks of 20, 50, or 100 birds, an observer could estimate fairly accurately the flocks of up to 2,000 birds at a time. At one five-acre roost three independent observers counted the numbers flying into the roost one evening toward the end of the 1962 season. The mean estimate of the number of birds using this one roost was 66,000 birds ±15,000, and this estimate was conservative.

Although I hoped that the retrapping of banded birds might also aid in estimating the population of the roost, only two of the 2,888 birds banded in the eight seasons (1959-1966) were retrapped: one was caught at the same roost three days after being banded; the other almost exactly a year later at a roost two miles from where it had been banded. No other banded birds have been recovered.

The time of the Dickcissels' arrival at the roost in the evening depended on the distance of the roost from the feeding grounds, the weather, and the time of year.

Between early January and late April the time of sunset varies by only 23 minutes in Trinidad—16 minutes in January, 7 minutes in February, and hardly any in March and April.

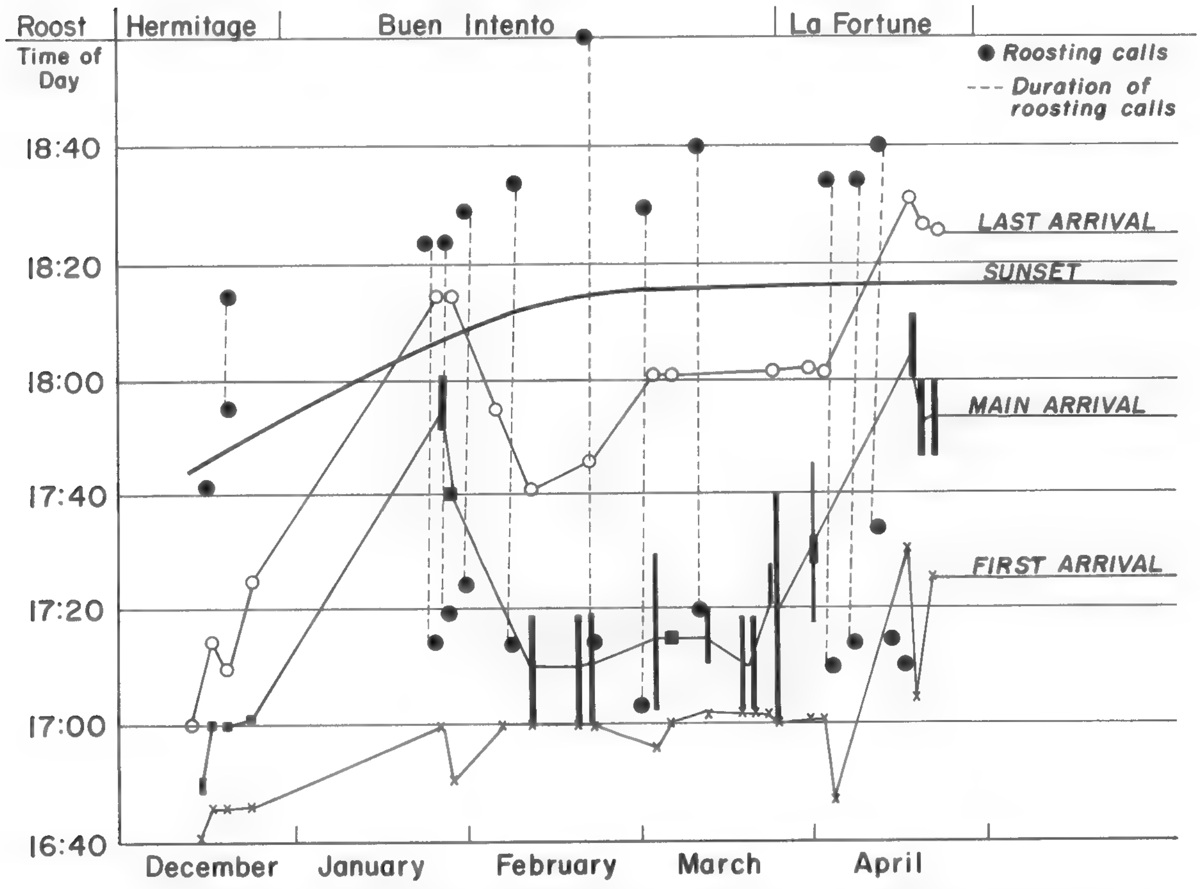


Figure 3. The times of arrival at the roost and the duration of the roosting calls of the population from the Aropuche Lagoon in 1962-1963. This population changed roosts twice that season. In the last few weeks before migration the arrival was later and the roosting calls almost ceased.

Figure 3 shows the times of arrival at the roosts of the birds (Oropouche Lagoon population; see map, Figure 1) feeding in the 1962-1963 season. It happened that during this season the birds changed roosts several times: during December they roosted near the feeding grounds at Hermitage; during January, February, and part of March they transferred to the Buen Intento roost, 15 miles distant; the last month (mid-March to mid-April) they moved back to the lagoon, to the La Fortune roost. The birds that fed in the foothills did not transfer from Buen Intento to La Fortune until late March. Because of the distance from the main feeding area, the times of arrival are all later at Buen Intento than at Hermitage until mid-March. After that time only the local population came to Buen Intento and arrived earlier.

Rain showers that kept the birds hidden in shelter at the feeding grounds sometimes delayed the arrival at the roosts; or an overcast day with intermittent showers sometimes caused them to roost early. Normally the weather was fine.

The arrival time was significantly later the last few weeks before spring migration (mid-April) when the main body of birds came in only a few minutes before sunset and quite a few arrived after sunset. This coincided more or less with the increase of weight. During this period I caught birds arriving at the roost with their bills still choked with grain, giving the impression that they were feeding up to the last possible moment.

The time of departure from the roosts in the morning followed a steady pattern (see Figure 4). Throughout January, February, and March the movement was concentrated into a short period some 25 minutes after sunrise. During the last three weeks before migration, however, the Dickcissels left the roost less than 15 minutes after sunrise; and, at the very end of their stay, all of the birds left before sunrise. The weather, invariably clear at dawn at this time of year, could not have been a factor causing them to leave earlier. The departure involved much less time than the arrival and, on occasion, was spectacular—as when perhaps 100,000 birds flew out of a canefield in a little over two minutes.

Occasionally in the evening I watched the feeding areas as the Dickcissels massed to fly to the roost. Sometimes separate flocks of from 30 to 50 birds made the journey; more commonly the flocks amalgamated, wheeling over the feeding grounds, settling, flying up again before they eventually made for the roost at the usual time. I frequently saw flocks of from 2,000 to 3,000 rise and leave at one time. When the journey was a long one—for example, over 15 miles from the Oropouche Lagoon to the Buen Intento roost—the flocks sometimes amassed into one continuous column, 20 to 30 birds wide, stretching for up to a mile, and resembling, from a distance, a swarm of locusts. I roughly estimated one such column as containing over 35,000 birds.

Normally, as they flew to the roost, the birds traveled at a fairly constant height, 200 to 300 feet above the ground. Over undulating country and as they neared the roost, some flocks flew closer to the ground, occasionally embarrassing the mist netter with a bag of 50 individuals at one time. The speed of travel also seemed to be fairly constant when flying to the roost. I timed one flock as it flew alongside a road into a light prevailing wind as moving about 45 miles per hour. Very late in the season the birds seemed to fly much more slowly.

On arrival at the roost area and reaching a point directly above the roost, the flocks traveling at about 250 feet broke formation and cascaded very rapidly into the sugarcane, making a great deal of noise as the air rushed through their wing feathers. Sometimes a flock, approaching a roost just above

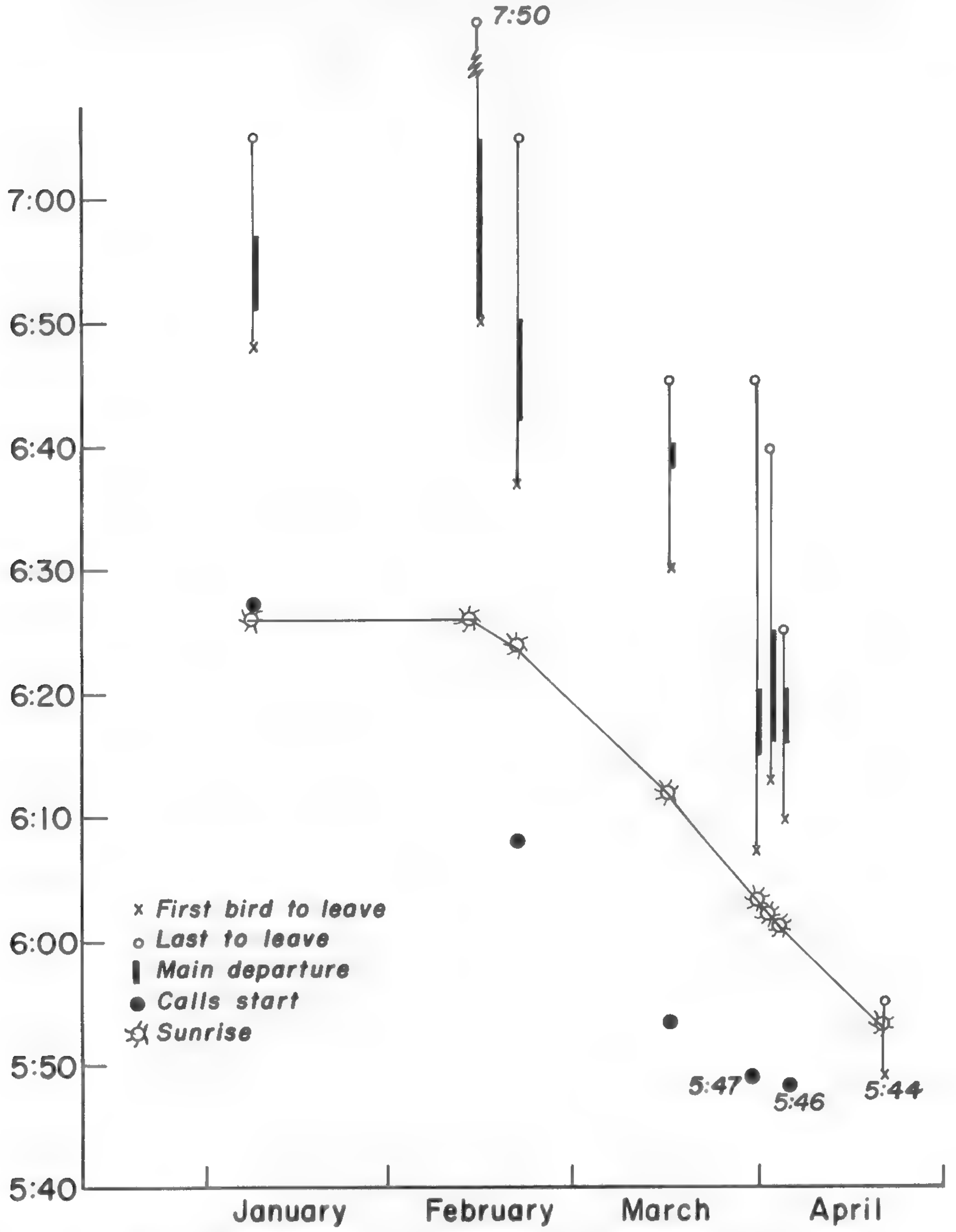


Figure 4. The times of the beginning of roosting calls and the departure of the Dickcissels from the roost in the morning. For most of the season the roosting calls began about 20 minutes before sunrise and the birds left about 25 minutes after sunrise. About three weeks before migration they departed about 15 minutes before sunrise and at the very end they all left before sunrise.

the ground, entered the cane some distance from the roost and filtered gradually through the cane or moved in short flights to the roosting sites.

In the morning the birds generally left together in a mass, except for a few isolated individuals or small bands of less than 30 birds. As soon as the first large flock went up, there was a more or less continuous movement of flocks funneling high up—to 400 or 500 feet—and then disappearing in the direction of the feeding grounds.

In some cases—for example, at Buen Intento, where one roost served two distinct feeding areas—the birds departed simultaneously, flying in two different directions from different sections of the roost.

During the day the roost was empty of Dickcissels. Few other species of birds inhabit the sugarcane in Trinidad. Those include the Ruddy Ground-Dove, the Masked Yellowthroat (*Geothlypis aequinoctialis*), and the Blue-black Grassquit.

Change of Roosting Sites

The changing of roosts that occurred in 1962-1963 prompted a survey of the location and nature of the roosting sites. It seemed strange that the birds feeding in the Oropouche Lagoon should travel over 15 miles to and from the Buen Intento roost daily when the entire country between the feeding area and the roost was planted with sugarcane. La Fortune (see Figure 1) was the nearest patch of cane to that part of the lagoon where the birds fed and from La Fortune to Buen Intento there is more or less uninterrupted sugarcane. Most of the Dickcissels roosted in the gently undulating country characteristic of the land bordering the flat lagoon, but one roost, the Debe roost, was in a patch of sugarcane on flat land in the lagoon itself, at a point where drainage permits crops other than rice and watermelon.

I investigated the varieties of sugarcane and learned that they were different at the various roosts. That at Buen Intento was unusual (B 48231) and differed from the varieties at the other roosts. However, B 48231 had also been planted in areas where Dickcissels did not roost. Although tradition seemed to be the only likely factor determining the choice of roosting site, I found it impossible to trace the history of any of the roosts.

The sugarcane is normally burned at nightfall before reaping the following day. This burning takes place during the period that the Dickcissels are in Trinidad and a roost is sometimes burned after the birds have entered it for the night. Usually the preparations for the fire, the smoke, and the noise of the burning cane alarm the birds so that they fly out in good time, scatter temporarily, find shelter nearby for the rest of the night, and settle in a new roost on the following evening. Once, according to one farmer, a roost was burned from all four sides at one time and many of the birds perished. They might have escaped by flying straight up and over the wall of fire but this they apparently did not do.

The burning of cane cannot explain the change of roosting site in 1962-1963 since the birds, in both cases, moved before the fields were fired.

Behavior at the Roost

When the Dickcissels settled into the sugarcane in the evening, they moved about, each seeking a perch. The flocks alighted in the most thickly populated patch and filtered outward until they found room. At this time of the year the cane varies in height from 10 to 12 feet. About eight feet above ground the leaves part from the stems, and the birds perched on these leaves, bent nearly horizontal, in closely packed rows with often as many as 12 birds on a leaf. I never observed Dickcissels perching less than six feet above the ground, which may have been a factor in reducing the predation of snakes, rats, and mongooses (*Herpestes javanicus*). The distribution of birds on a perch appeared to be quite haphazard with males, females, and immature birds grouped in different proportions and often changing perches early in the evening.

Soon after sunset their movements largely ceased. A nearby fire or heavy rain naturally disturbed them to some extent. I shall describe the disturbances by predators below. But by and large, during most of the night, an observer could walk quietly along a path through the cane and never know that he was surrounded by thousands of roosting birds.

One noticeable feature of the Dickcissel roost was the incidence of vocalization. Apart from the normal flight-call, described above as a grating *bjjt,* I heard no other call by Dickcissels arriving at the roost. Some minutes after settling they gave a call which consisted of several vocalizations—an incisive *jeep,* a chattering *je-je-je,* rather reminiscent of the House Wren, and most characteristically a sibilant *tsiulp* or *tsirrup.* I have described these vocalizations as the roosting call.

As soon as some individuals had taken up the roosting call, the chorus swelled until it took on a unified texture of its own, resembling a highly amplified hissing sound and clearly audible on a still evening three-quarters of a mile away.

During most of the season the roosting call started some 20 to 30 minutes after the first birds arrived and more or less coincided with the arrival of the main body (see Figure 3). Early in the season it tended to be faint, as if not yet established; at the end of the season, shortly before departure, it became much less pronounced until it was almost non-existent when the population dropped to a low level.

Early in the morning the birds rendered the roosting call before departing for the feeding area (see Figure 4). During most of the season the call began about 20 minutes before sunrise, 40 minutes or so before the birds left. It too was less pronounced or lasted for a shorter time at the beginning and end of the season.

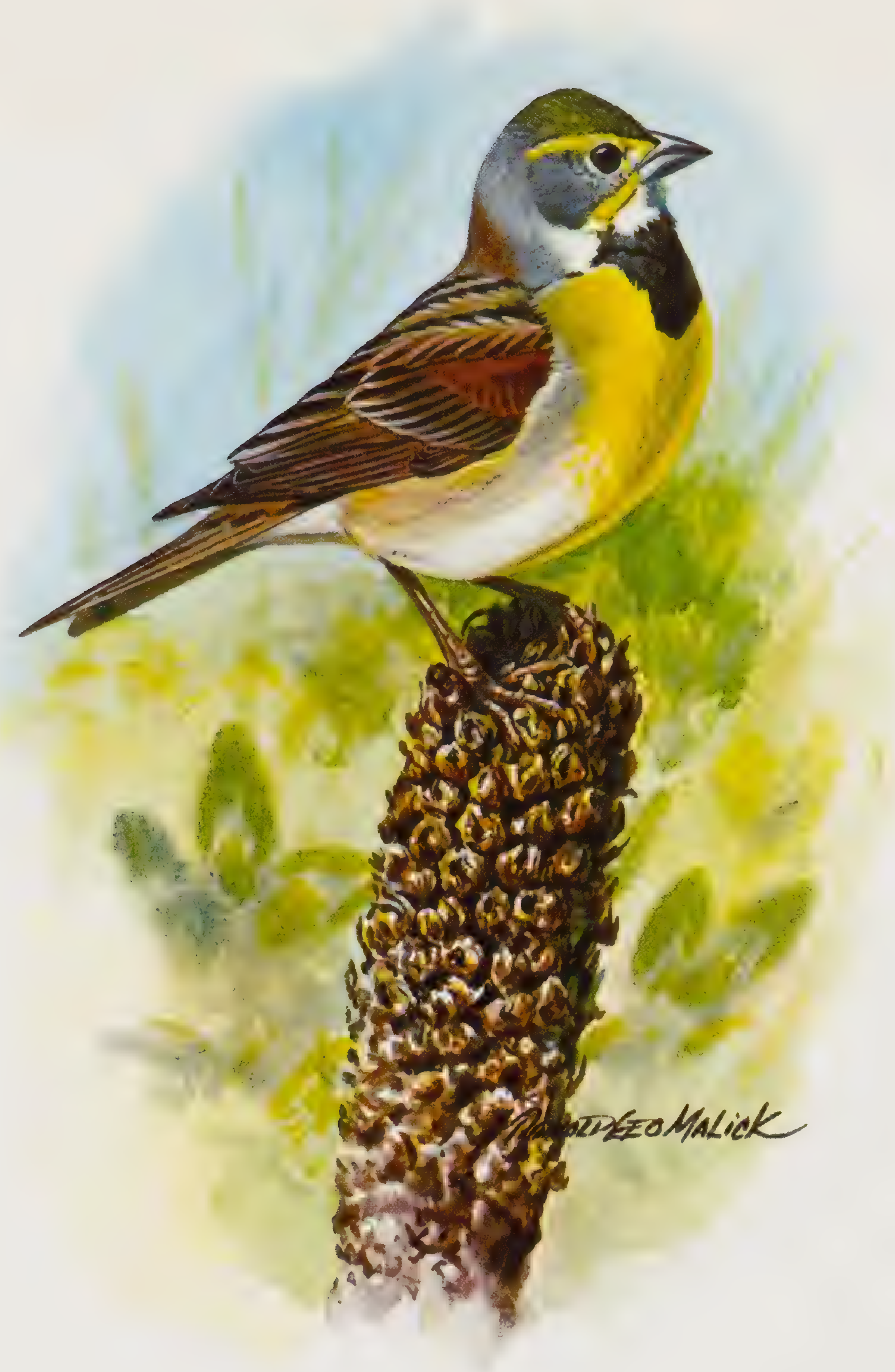
Predation at the Roost

Not surprisingly such a concentration of birds attracts predators and I paid constant attention to the incidence of predation. Definite predators included the Merlin or Pigeon Hawk (*Falco columbarius*), the Aplomado Falcon (*F. femoralis*), the Barn Owl (*Tyto alba*), and man. In addition, I observed the mongoose and domestic cat near the roosts and, on occasions, the Gray Hawk (*Buteo nitidus*). The behavior of the Gray Hawk and the Dickcissels did not indicate that this hawk was a predator.

Man was not an important predator. Very rarely the inhabitants of nearby villages raided the roosts at night, trapping a stray bird for a pet, or killing numbers by torchlight. In my experience, this seldom happened. For one thing, the birds, panicked by the glare of the torchlight and flying aimlessly about, were difficult to see; and for another, the small size of the prey discouraged all but the most desperate hunters. At the feeding grounds in the daytime, gunners have been known to fire small shot into closely packed flocks, killing as many as 70 birds with one blast. Here again the size of the prey hardly makes it worth the effort.

On two occasions, I saw the Aplomado Falcon, a bird that occurs rarely in Trinidad (ffrench and ffrench, 1966), hunting Dickcissels and bats (*Molossus* sp.) on the edge of the roost. Unfortunately I could not be sure that the falcon caught a Dickcissel.

I recorded at least one Merlin, a winter visitor to Trinidad, on almost every visit to the roost between 16 December and 17 April. Rarely did I see as many as five at one roost; usually there were no more than two. However, I trapped four Merlins, all different individuals, at the Buen Intento roost between 26 January 1963 and 29 March 1964. The regularity of the attendance of the Merlins at the roost, always when the birds were there and never at other times, gave the impression that Dickcissels formed the staple diet of these falcons. Further evidence came from under their feeding trees where we picked up pellets containing no recognizable remains of anything except Dickcissels.



Painting of Dickcissel by Donald Leo Malick

One might expect that a Merlin would have no difficulty in catching a Dickcissel out of a flock of several hundreds approaching or leaving the roost. Frequently, though, I watched a Merlin dive into a flock of birds, scatter them in all directions, and emerge with no victim. Perhaps the very numbers of the prey and their flurrying movements confused the falcons; possibly it was the evading action of the Dickcissels on the approach of the raptor. But the Merlins had another method, probably more successful. They flew a few feet above the ground along the track between the canefields and caught the stray individuals that were constantly crossing from one patch to another. I noticed that the roosting calls ceased whenever a Merlin circled above the roost and that the Dickcissels were silent as long as the Merlin remained in view.

I saw the Barn Owl, the other main predator and a resident in Trinidad, at all the different roosts, and two Barn Owls hunted regularly at Buen Intento. The owls, unlike the Merlins, never hunted by daylight. They came to the roost after sunset and often stayed for hours. During one night, 16 March, they hunted until after midnight; on other occasions I saw them early in the morning before sunrise.

They flew low over the canefields and plunged suddenly into a group of roosting birds, causing a great disturbance. Judging from the fact that these disturbances occurred regularly every minute or so for long periods, the owls were frequently unsuccessful. Their attacks provoked modified versions of the roosting call at any hour. The *je-je-je* alarm call predominated and might continue for some time after the owl had moved on.

Significance of the Communal Roost

With the constant predation not only by hawks and owls but probably by snakes and mongooses as well, of what advantage is the communal roost to the Dickcissel? There are plenty of individual roosting sites near the feeding grounds where, it would seem, the birds would be much safer at night.

Ward (1965) suggests that the main advantage of communal roosting to birds in the tropics is the provision of an "information centre" where "knowledge" of good feeding places may be shared within a species which feeds over a large area. He applied his hypothesis in the first instance to an African weaverbird, the Black-faced Dioch (*Quelea quelea*) and noted that when the roost emptied in the early morning, large parties of these birds would fly a short way and then perch, joining other groups as they left later. Thus the birds, which had been unfortunate in their feeding areas the previous day, could join other birds whose behavior indicated that they were returning to profitable feeding grounds.

While this phenomenon has not been noted in the Dickcissels in precisely the same way, the same advantage might accrue to roosting Dickcissels. Certainly the roost empties much more quickly in the morning than it fills in the evening. The flocks are much larger in the morning; sometimes the entire population, with only individual exceptions, leaves in one or two flocks. Thus, the birds that had not fed well the day before could follow or join those that were returning to good feeding areas.

The only time when the Dickcissel roost empties gradually is at the beginning of the species' annual visit to Trinidad. In early January I have found sizable flocks still in the roost one hour after the main departure. This too fits Ward's hypothesis for at this time of year the rice has just been reaped or is still standing and food is abundant. As the dry season advances, food becomes scarce and it must be increasingly difficult for the birds to find good feeding places.

Migration

Owing to the disturbance caused by the Barn Owls, I could not measure accurately the amount of nocturnal unrest associated with the approach of spring migration in April. However, I did observe some unusual behavior on several occasions in mid-April.

The end-of-season behavior at the roost was characterized by a noticeably slower approach to the roost in the evening and by a diminution, or cessation, of the roosting calls. Also, I noted that some flocks, after settling in the evening, tended to leave the roost and fly off in some direction for a half-mile or so before returning to settle again. The birds never did this earlier in the season.

On about 17 April in a typical year, I noted the following premigration behavior. Having finally settled at the roost at about 1800 hours, the birds maintained a silent period for a few minutes, followed by a gradually increasing restlessness. Finally, at five minutes after sunset (approximately 1820) almost the entire roost appeared to be in an uproar, caused not so much from the noise of the roosting calls as from the sound of the constant wing movements of thousands of individuals flying singly or in flocks from one part of the roost to another. As darkness came, the restlessness gradually subsided. By 1835 there was almost complete silence and lack of movement. A few minutes later, still in almost complete silence punctuated only by the occasional *bjjt* flight-call, I saw bands of up to 100 birds silhouetted against the western sky as they rose slowly and steeply out of the canefields and headed due west toward northern Venezuela. After some thousands had left in only a few minutes, the exodus ceased and complete silence prevailed, interrupted only by the sound of wing-flutters as a Barn Owl dived into the roost. On the following nights this procedure was repeated until the numbers became too small for me to observe easily.

For a number of reasons I can safely assume that the Dickcissels trapped as they left the roost after mid-April were individuals starting on a journey of some thousands of miles. At no other stage of the season did I observe Dickcissels leave the roost after settling for the night except in case of fire; there are no observations of Dickcissels leaving Trinidad at any other time of day; and I have never seen any Dickcissels arriving at a roost after dark.

Data from Captured Birds

From the large number of captured birds I amassed considerable data, principally on the ratio of males to females and of adults to immatures, wing measurements, weights, and stages of molt.

Each year the males made up almost two-thirds of the birds caught (see Table 1). The percentage for the entire season was about evenly two-thirds until at the very end—around 10 April—when the percentage of males dropped steeply, indicating that the males migrated earlier than the females. J. L. Zimmerman (pers. commun.) reports that the males precede the females on the breeding grounds in Illinois by five days.

I could generally distinguish the first-year birds from the adults by the presence of yellow at the corners of the closed gape. In addition, the lesser secondary coverts of the first-year birds were dull brown or olive instead of the

TABLE 1

Number of Dickcissels Trapped in Trinidad During Study Period

Year	*Number of males*	*Number of females*	*Percentage of males*
1959	300	132	69
1960	527	268	66
1961	238	123	66
1962	134	65	67
1963	302	113	73
1964	154	81	65
1965	144	76	65
1966	161	69	70
Totals	1960	927	68

rich chestnut of the adult. The method of aging by skull ossification I found inapplicable since by the time the birds reached Trinidad the skulls of even the most obvious immature birds were, with few exceptions, fully ossified. By the end of the season it was probably even more difficult to be certain of the age distinctions. The estimates of adult and immature birds in seven years (1959-1965) showed an over-all average of 73 per cent of adults to 27 per cent immatures with annual variations of adults ranging from 61 per cent to 88 per cent. Thus the adults outnumbered the immatures by about two or three to one.

On the whole it was easy to distinguish adult males from females because of their larger size, longer wing, greater weight, and brighter coloration. In addition, the plumage of the throat and breast was diagnostic. Typically, the male wore a white "mustache" streak tinged with yellow and a large black throat-patch. The female had a white mustache streak bordering a white or yellow throat. She had no black throat-patch, only a few dark streaks extending down onto the breast. Some individuals, which showed small black throat-patches, possessed otherwise typical female characters. Upon dissection, a number of these intermediate individuals proved to be females.

The most reliable characteristic was a combination of wing length and throat plumage. The wing length of 141 typical males (using the natural chord of the wing to the tip of the longest primary without flattening the wing) averaged 82.8 mm (77 to 89 mm, SD 2.03). A group of 74 typical females averaged 74.7 mm (71 to 80 mm, SD 1.66).

I captured most of the birds as they flew into the roost in the evening and weighed them at once, using a calibrated spring balance, accurate to 0.5 gm. The weights of both males and females were fairly constant on the average from the beginning of the season up to the end of March (see Figure 5). Thereafter the Dickcissels gained considerable weight due to the deposition of fat preceding the spring migration. Birds dissected before March showed very little fat; those taken in mid-April were extremely fat. At migration time the males averaged a 56 per cent increase over normal weight with some individuals weighing 70 per cent more. Females averaged 51 per cent increase at the end of the season with individuals reaching a weight 65 per cent above the midwinter norm.

Whenever catches of wild birds were made early in the morning following an evening's catch, the average weight of both sexes was lower by between 2.5 gm and 3.5 gm, or about 10 per cent of the body weight. Forty birds, kept in captivity between 1700 and 0700 hours, lost from 1.5 gm to 5.5 gm. It was, however, impossible to simulate natural conditions for these captives and most likely many spent the night in constant motion.

The weight gain preceding migration was noticeable in wild birds during the last few days of March. In males this rate of increase accelerated sharply from the beginning of April, reaching a peak by mid-April (see Figure 6A). Females too began to gain weight the last few days of March but their sharp increase in weight came about the second week in April. Zimmerman (1965:58) found that Dickcissels migrating through the Canal Zone did not show increased weight. He believed that these birds, caught in the early morning, might have lost weight by a night of movement, or that the maximum fat deposition might occur later in the migratory journey. It now seems clear that Dickcissels migrating from Trinidad start at the peak of fat deposition and gradually use up this fat on the journey.

Figure 6B shows a rather different picture for captive birds, confined in an outdoor, roofed aviary with plenty of flying space and provided with unlimited seeds and water and occasional live insects. The males began to gain weight after January; the rate of increase accelerated beginning in early

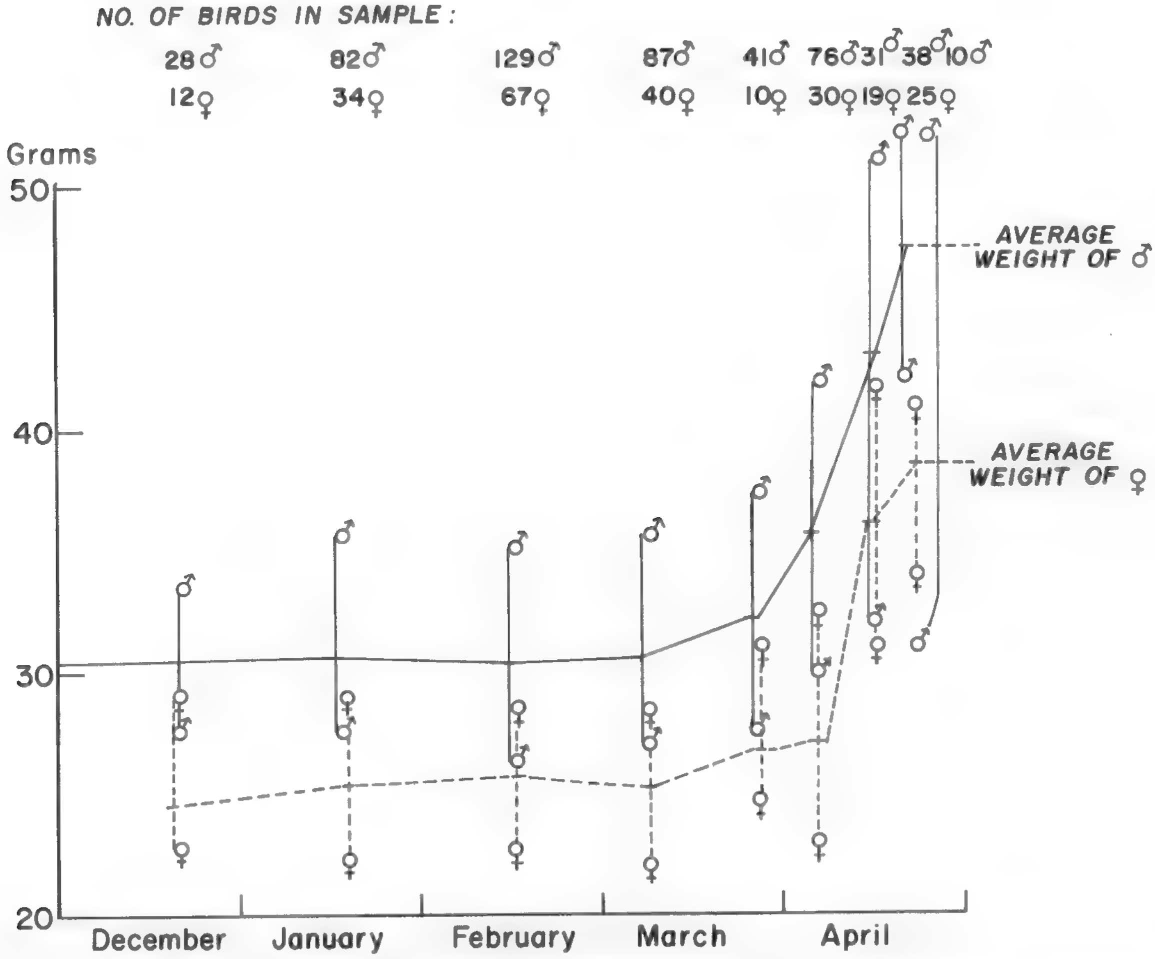


Figure 5. Weights of male and female Dickcissels trapped in Trinidad during the winter season. The weights increased sharply just before migration.

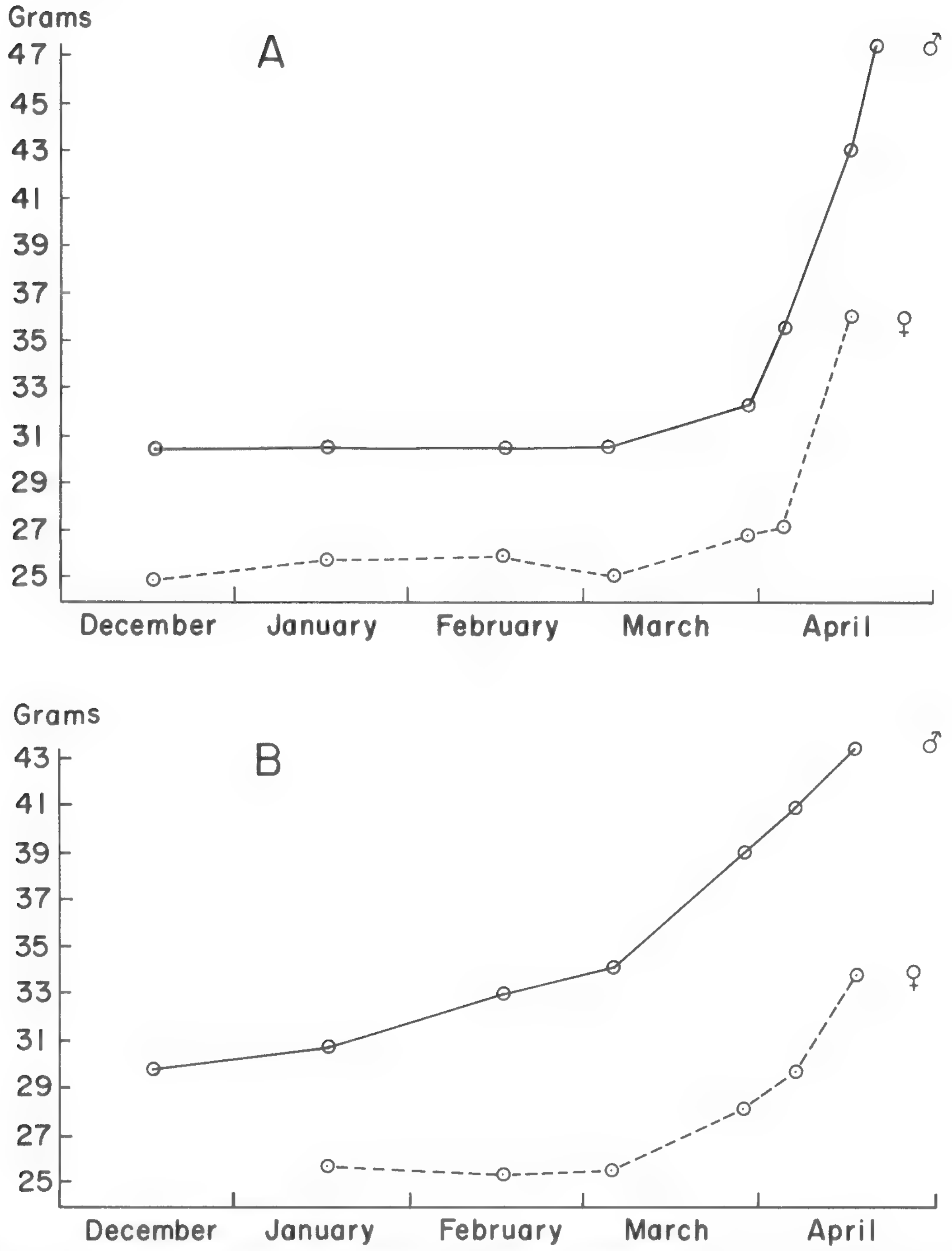


Figure 6. A. Weights of male and female Dickcissels trapped in Trinidad in the winter. The males started to gain weight about one week before the females. B. Weights of captive male and female Dickcissels in Trinidad in the winter. The captive males began to gain weight in mid-January.

March; and their weights were equal to those of wild birds by mid-April. The females, always less aggressive than the males, maintained their normal weight until early March. Then they too showed an accelerated increase of weight earlier than the wild birds.

I examined all captured birds for signs of prenuptial molt. Unfortunately only one bird was ever captured twice in the same year, so I could not make comparisons. The captive birds were useless in this respect because, in the abnormal aviary conditions, molting may or may not have been normal.

The prenuptial molt for the adults involved the head, body, tail, scapulars, and some of the secondary coverts. The birds were already molting some feathers when trapped soon after their arrival in December. Dickcissels molted most heavily in February. Some males showed fine new plumage as early as 6 February; some females finished molting by 20 February, while, in others, new rectrices appeared as late as 18 April. Table 2 indicates the incidence of molt

TABLE 2

Comparative Molt in Adult Dickcissels[1], 1963

	Date	Sample	Head	Back	Under-parts	Scap-ulars	Coverts Lesser	Coverts Median	Coverts Greater	Tail
Males	6 February	12	83	83	92	83	67	0	0	67
	6 March	12	8	42	25	33	33	8	0	42
	3 April	13	23	8	16	0	0	0	0	8
Females	6 February	6	100	100	100	83	33	0	0	83
	6 March	5	40	40	40	60	60	20	20	40
	3 April	5	40	20	60	20	20	20	20	40

[1] The figures show the percentage of sample in molt.

by body region in the two sexes. Females lagged slightly behind the males. Of 103 birds examined between 9 and 19 April 1965, four of 69 males (6 per cent) and eight of the 34 females (24 per cent) were still molting head or body feathers.

Zimmerman (1965) reported a significant correlation between the prenuptial molt and a drop in body weight in the Dickcissel and other species. Despite the very large numbers of Dickcissels that I examined in Trinidad, I found no correlation. While the molt was usually over by the time the weight increase began, no appreciable drop in body weight occurred during the molt period. Figure 7 gives a random sample of the weights in grams of birds in heavy molt as compared with birds that showed no molt on the same day. Neither group shows much divergence from the average. One can only conclude that while certain birds may lose weight during the molt period, it is by no means the general rule.

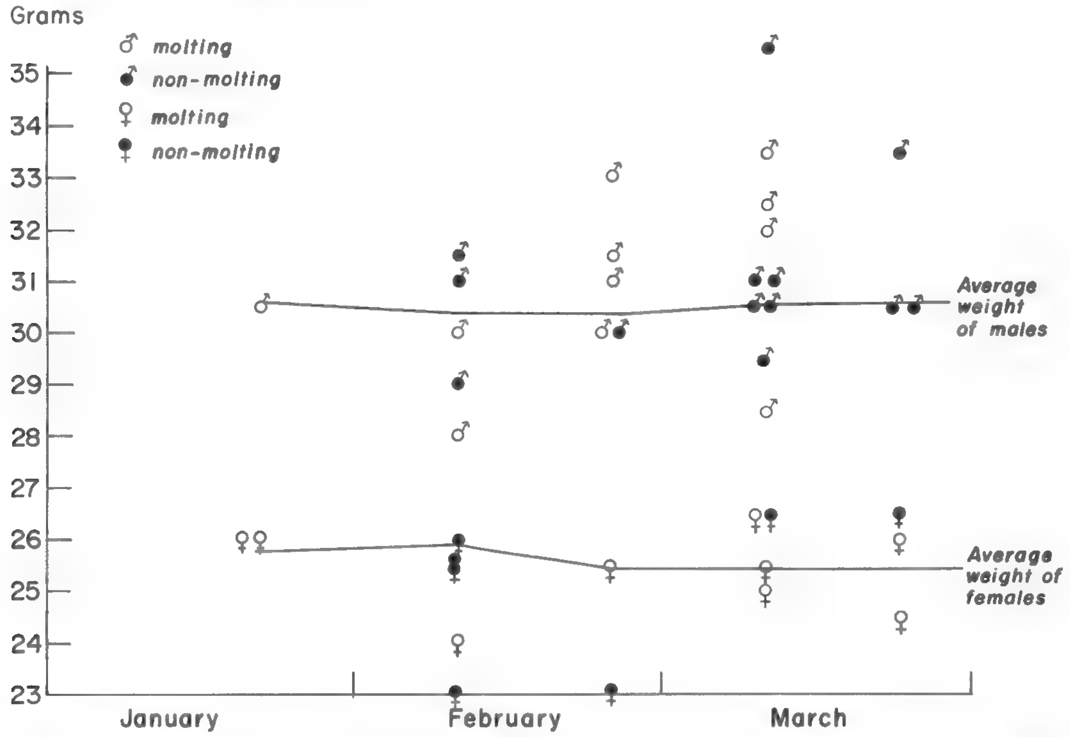


Figure 7. A random sample of weights of birds in heavy molt compared with weights of birds showing no signs of molt on the same day. There appears to be no appreciable drop in body weight during the period of molt.

Summary

Dickcissels (*Spiza americana*) have been recorded wintering in Trinidad during the last 100 years, but possibly not consistently. They have wintered regularly during the period of this study from 1959 to 1966.

I trapped and banded 2,888 birds in Trinidad during the study period and observed their feeding, roosting, and migratory behavior.

Dickcissels migrate to and from Trinidad through Central America, Colombia, and Venezuela, visiting Trinidad from December through mid-April.

The principal food of the Dickcissel is rice, but it also includes the seeds of wild grasses. Distribution in Trinidad centers on the rice-growing areas. No distinct associations are formed with other species.

Large numbers of Dickcissels congregate in fields of sugarcane to roost. Generally, birds arrive at the roost 45 minutes to one hour before sunset, but just before migration their arrival is much nearer sunset. Similarly, departure from the roost in the morning is about 25 minutes after sunrise, but much earlier as migration time approaches.

The birds' roosting sites are probably traditional, but the birds sometimes interchange between them. I have described the methods of roosting and the regular vocalizations at the roost.

The two most important predators on the Dickcissels are the Merlin and the Barn Owl, both at the roost. I have described their method of hunting.

I have suggested that the function of the communal roost may be to provide an "information centre" where "knowledge" of good feeding places is shared.

Actual migration was observed, starting from the roost soon after dark in mid-April in a westerly direction.

Data from captured birds are tabulated. Males outnumbered females by about two to one, but left a little earlier on migration. First-year birds were distinguished from adults by yellow at the corners of the closed gape and brown, not chestnut, lesser secondary coverts. Females generally had white, the males black, throats, but exceptions were found. In addition, females had wing lengths averaging 74.7 mm, while males averaged 82.8 mm. Weights of birds were constant until the last three weeks before migration, when a considerable increase took place, averaging over 50 per cent above the winter norm. Some captive birds also gained weight during the winter season, but considerably earlier than the wild birds. The prenuptial molt is described. It is heaviest in February. No significant correlation was found between heavy molt and a drop in weight.

Acknowledgments

In this study I received help of various kinds. For assistance in the field, I wish to thank especially my wife and also J. B. Saunders, J. S. and J. Griffin, and several others. For advice, information, and helpful comment I must thank John L. Zimmerman, David W. Snow, Charles T. Collins, Alfred O. Gross, Paul Schwartz, Thomas H. G. Aitken, G. D. Smooker, William H. Phelps, Jr., Derek Fewkes, Ian Lambie, and Paul Patrick, and also the Director of the Meteorological Service in Trinidad. I also thank the staff of the Department of Ornithology, American Museum of Natural History, for allowing me to use study skins, which I did while holding a grant from the Frank M. Chapman Memorial Fund.

Finally, my thanks go to J. B. Saunders and Charles T. Collins for criticizing the draft of this paper and offering several helpful suggestions.

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SONGS OF THE YELLOWTHROAT

DONALD J. BORROR

The advertising songs of passerine birds vary in extent and character within different species (Borror, 1961). An outstanding example is in the songs of the Yellowthroat (*Geothlypis trichas*), a bird with a wide geographical range and considerable variation in form, size, and color. As many as 11 subspecies or races are recognized as occurring in North America north of Mexico. The approximate breeding ranges of these subspecies in conterminous United States are shown in Textfigure 1.

The songs of the Yellowthroat consist of a series of similar phrases. Although each individual has just a single phrase in its vocabulary, different Yellowthroats often sing different phrases. This paper reports the nature and extent of variation in the songs of Yellowthroats and speculates on the significance of the variation.

I analyzed 472 recordings of Yellowthroat songs from 30 states and six Canadian provinces. Of these, 61 were from the Laboratory of Ornithology at Cornell University, 26 were made by J. E. and N. J. Stillwell, three by W. W. H. Gunn, and the others were my own, now a part of the collection of recorded animal sounds of the Department of Zoology and Entomology at Ohio State University.

I believe these recordings represent the songs of 411 individuals. The number may be smaller. Saunders (1938:122) states that the songs of an individual Yellowthroat may vary from day to day. However, of the hundreds of Yellowthroats I have listened to and of the more than 300 I have recorded, not one, except for the few birds that used two or three different phrases *in the same song,* changed its phrase. I have heard birds continually singing the same phrases throughout the season and never changing. I therefore assume that each different song in the 472 recordings represents a different bird.

The Notes in Yellowthroat Songs

I use the term "song" for the advertising vocalization most commonly paraphrased as *wich-i-ty wich-i-ty wich-i-ty.* There are several other paraphrasings (Gunn and Borror, 1957:35). Saunders (1935:211) states that the song normally consists of 3-, 4-, or 5-note phrases repeated three or four times, and that 2- and 6-note phrases are rare.

A note, used here, is a sound that produces a continuous, or nearly continuous, mark on the sound spectrogram. Each syllable in the paraphrasing above represents a note. Davis (1964) called these notes "figures" because they are nearly always slurred. I prefer the term "notes" and refer to a group of notes, repeated two or more times, as a "phrase."

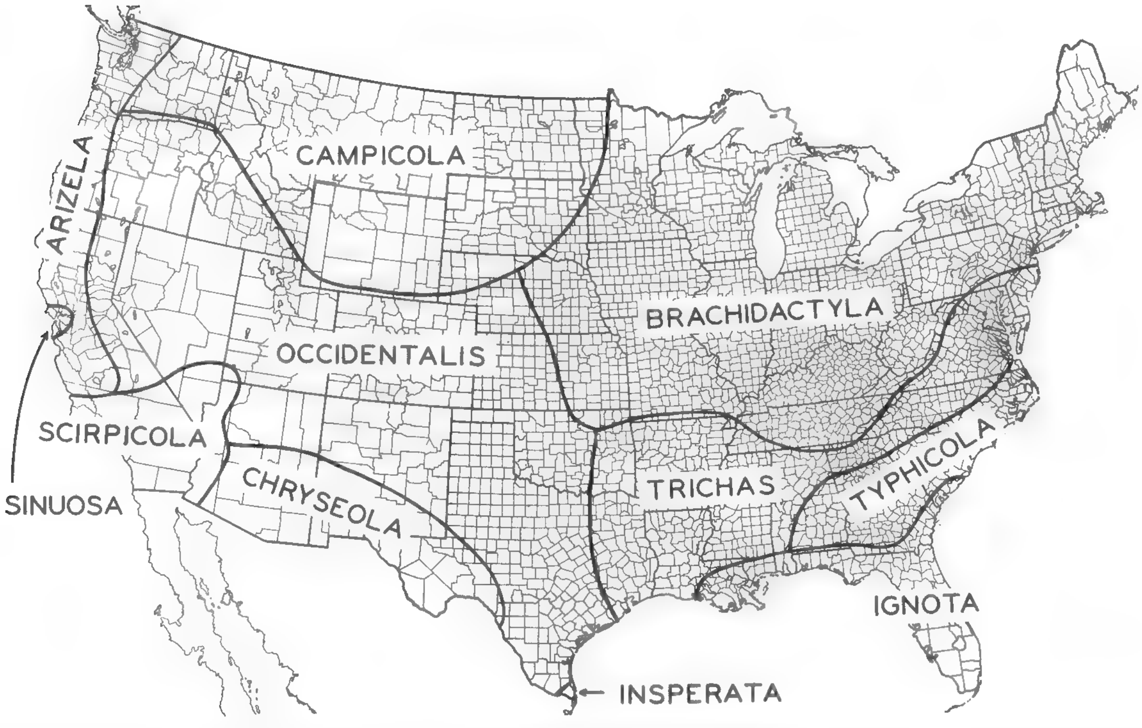
Species-specific Features of Yellowthroat Songs

Yellowthroat songs, in spite of their variation, can nearly always be recognized because of certain distinctive features: the general form, the character of the notes, and the singing habits of the bird.

The song normally consists of from two to five repetitions of a given sequence of notes, a phrase, uttered relatively slowly, from three-quarters of a phrase to three phrases per second and, on the average, about two per second. The individual notes, relatively loud and usually uttered slowly enough to count, consist of simple slurred elements. There is no rapid frequency modulation, hence no buzzy quality. The pitch of most songs lies between 3,000 and 7,000 cycles per second (cps); a few contain frequencies as low as 2,000, a few as high as 9,000 cps. Songs in the pitch range of the Yellowthroat do not have the lisping quality of other warblers that are higher pitched.

Practically all the notes in the songs are simple, made up of a fundamental and harmonics. They consist of from one to five elements, each of which, according to Davis (1964), is a single slur either up or down, and I have classified them as follows:

1D — a downslur (Figures 1–11)
1U — an upslur (Figures 12–21)
2D — a downslur followed by an upslur (Figures 22–33)
2U — an upslur followed by a downslur (Figures 34–55)
3D — down-, up-, and downslurs (Figures 56–61)



Textfigure 1. Map showing the approximate breeding ranges of subspecies of the Yellowthroat in conterminous United States.

TABLE 1

Phrase Variation in Yellowthroat Songs

Area and subspecies	*Number of birds*	*Notes per phrase*[1]					*Total birds*[2]	*Total phrase types*	*Birds per phrase type*
		2	*3*	*4*	*5*	*6*			
Northeastern									
brachidactylus									
New England and Maritime Provinces		2	35	42	37	1	111		
		1.80	31.53	37.84	33.33	0.90			2.78
		1	15	13	10	1		40	
Quebec	2								
New Brunswick	2								
Maine	101								
New Hampshire	2								
Vermont	4								
		0	9	13	3	0	25		
Ontario and New York		–	36.00	52.00	12.00	–			2.08
		–	5	6	1	–		12	
Ontario	7								
New York	18								
		13	159	17	3	0	190		
Midwestern		6.84	83.68	8.95	1.58	–			3.39
		6	34	14	2	–		56	
Michigan	7								
Ohio	165								
Kentucky	1								
West Virginia	8								
Western Maryland	1								
Western Virginia	2								
Wisconsin	1								
Minnesota	5								
		15	203	72	43	1	326		
Total[4]		4.60	62.27	22.09	13.19	0.31			3.26
		6	50	30	13	1		100	
Mideastern									
		9[3]	1	5	6	0	21		
trichas		42.86	4.76	23.81	28.57	–			2.33
		2	1	3	3	–		9	
Eastern Maryland	1								
Eastern Virginia	4								
North Carolina	7								
Alabama	1								
Arkansas[3]	8								
		0	0	1	1	0	2		
typhicola		–	–	50.00	50.00	–			1.00
		–	–	1	1	–		2	
Georgia	2								
		9	1	6	7	0	23		
Total		39.13	4.35	26.09	30.43	–			2.09
		2	1	4	4	–		11	
Southeastern									
		0	2	5	4	7	18		
ignota		–	11.11	27.78	22.22	38.89			1.50
		–	1	4	3	4		12	
South Carolina	4								
Florida	14								

TABLE 1 (continued)

Area and subspecies	*Number of birds*	*Notes per phrase*[1]					*Total birds*[2]	*Total phrase types*	*Birds per phrase type*
		2	*3*	*4*	*5*	*6*			
Western Plains									
		2	5	2	0	0	9		
campicola		22.22	55.56	22.2	–	–			1.00
		2	5	2	–	–		9	
Manitoba	1								
Saskatchewan	1								
British Columbia	1								
Montana	1								
North Dakota	2								
Northwestern Minnesota	1								
Eastern Oregon	1								
Wyoming	1								
		2	16	0	0	0	18		
occidentalis		11.11	88.89	–	–	–			3.00
		1	5	–	–	–		6	
Utah	1								
Colorado	16								
Western Kansas	1								
		0	4	0	0	0	4		
chryseola		–	100.00	–	–	–			2.00
		–	2	–	–	–		2	
Western Texas	1								
New Mexico	2								
Arizona	1								
		4	25	2	0	0	31		
Total		12.90	80.65	6.45	–	–			1.94
		2	12	2	–	–		16	
Far West									
		1	9	0	0	0	10		
arizela		10.00	90.00	–	–	–			1.67
		1	5	–	–	–		6	
Washington	1								
Western Oregon	8								
California	1								
		0	0	1	0	0	1		
sinuosa		–	–	100.00	–	–			1.00
		–	–	1	–	–		1	
California	1								
		1	1	1	0	0	2		
scirpicola		50.00	50.00	50.00	–	–			0.67
		1	1	1	–	–		3	
California	2								
		2	10	2	0	0	13		
Total		15.38	76.92	15.38	–	–			1.30
		2	6	2	–	–		10	
		30	241	87	54	8	411		
All birds[4]		7.30	58.64	21.17	13.14	1.95			2.98
		9	66	39	19	5		138	

---

[1] The upper figure is the number of birds; middle figure, the per cent of birds; lower figure, the number of phrase types.

[2] The songs of some birds contained two or three phrase types and were added to the total only when each phrase contained a different number of notes.

[3] The eight recordings from Fayetteville, Arkansas, lack information as to whether they are the songs of one bird or of several birds.

[4] Some phrase types were sung by two or more subspecies, or by birds in two or more areas.

3U — up-, down-, and upslurs (Figures 62–69)
4D — down-, up-, down-, and upslurs (Figures 70–73)
4U — up-, down-, up-, and downslurs (Figures 74–79)
5D — down-, up-, down-, up-, and downslurs (Figures 80–81)
5U — up-, down-, up-, down-, and upslurs (Figures 82–83)

The notes in each of these 10 types show considerable variation in the length of each element, the abruptness of the slurring, and the pitch. In determining the types I disregarded the slight "hooks" that sometimes occurred at the beginning or end of a note as in the beginning of the third note in Figure 125 and the fourth notes in Figures 122 and 124.

Most of the songs that I studied consisted of from two to five repetitions of a particular sequence of from two to six notes. The songs of 16 of the 411 birds were not so neatly arranged. These I considered atypical and shall discuss them separately. I represented the typical songs as follows:

2-note sequences:	A-B-A-B- — (Figure 105)
3-note sequences:	A-B-C-A-B-C- — (Figure 106)
4-note sequences:	A-B-C-D-A-B-C-D- — (Figure 107)
5-note sequences:	A-B-C-D-E-A-B-C-D-E- — (Figure 108)
6-note sequences:	A-B-C-D-E-F-A-B-C-D-E-F- — (Figure 109)

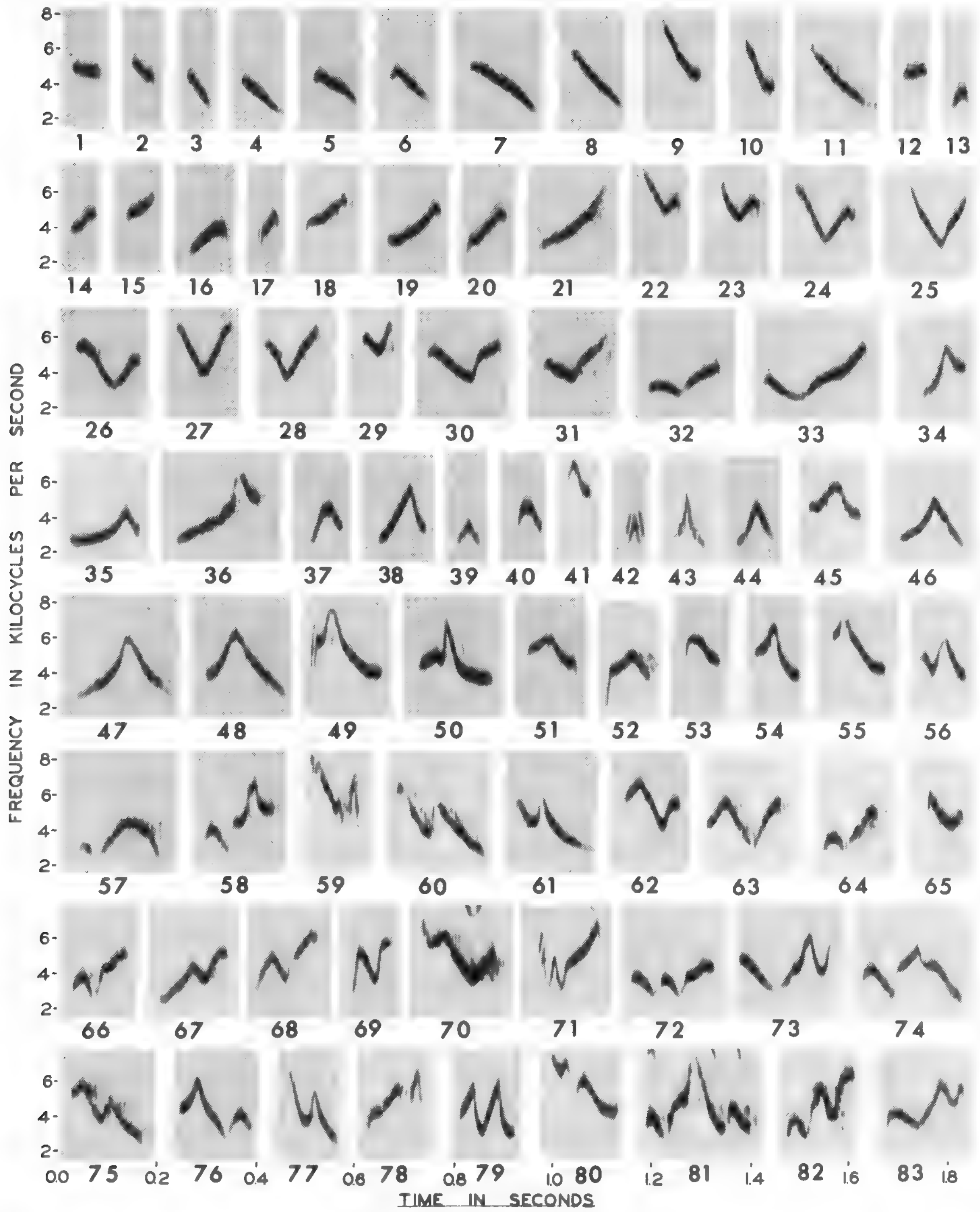
The interval of silence between notes was fairly uniform (Figures 84–127); only rarely was there a noticeably longer interval following one note of a sequence.

The number of notes in a given song was sometimes, but not always, an exact multiple of the number of notes in the phrase (Figure 109), and different songs of the same birds differed in this respect. The selection of one note as the first in the phrase was purely arbitrary. The bird might begin with Note A and end with Note F as in Figure 109, or the same bird might begin and/or end with any note from the middle of the phrase.

I base my delimiting of phrase type on the sequence rather than on the note in the sequence that I considered the first. For instance, in the 3-note song in Figure 106, A-B-C-A-B-C-A-B-C-A, the phrase could be A-B-C, B-C-A, or C-A-B. It appeared to me to be B-C-A, but I regard these three possibilities as representing the same phrase type, which I call Type 3–26.

The Phrases of Yellowthroat Songs

Using this method of analyzing the 472 recordings, I recognized 138 phrase types (Table 1) and classified them on the basis of the number of notes per phrase into five main groups. In each group I arranged the phrases in a sequence of an increasing number of elements per phrase. I then designated each phrase type by a two-number combination (example: 3–26). The first number represents the number of notes per phrase; the second shows the position of this phrase in the sequence, or the complexity of the phrase. The higher the second number, the more complex the phrase in relation to the other phrases in its group. Two-note phrases contained from two to nine elements; 3-note phrases, four to 11; 4-note phrases, four to 11; 5-note phrases, five to 13; and 6-note phrases, eight to 10.

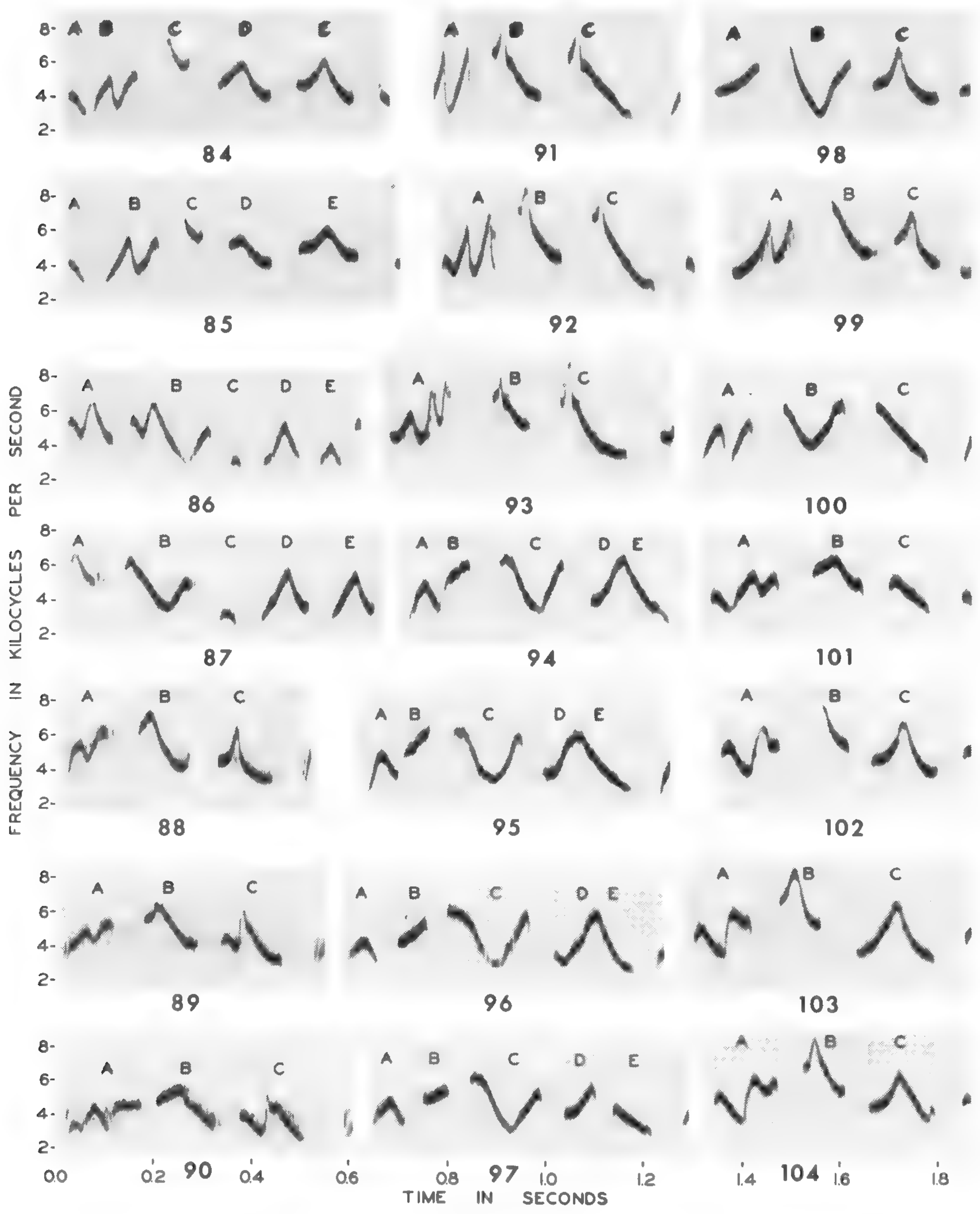


Figures 1–83. Sonograms of notes in Yellowthroat songs: 1–11, 1D notes; 12–21, 1U notes; 22–33, 2D notes; 34–55, 2U notes; 56–61, 3D notes; 62–69, 3U notes; 70–73, 4D notes; 74–79, 4U notes; 80–81, 5D notes; 82–83, 5U notes.

This classification sometimes obscured the similarities of phrases and I found numerous instances of very similar phrases, in some cases indistinguishable by ear, rather far apart in classification. Figures 86–87, 88–90, 91–93, and 102–104 illustrate four such instances where the phrases of birds, usually of a local area, were classified as different, yet differed only slightly in the character of one or two notes, and all were indistinguishable in the field. A few phrase types containing the same elements were classified as different because certain of those elements were connected in some notes and separated in others. Figures 84–85 and 94–97 illustrate two such instances; these phrases could be distinguished in the field only by careful listening.

Phrase Difference in Different Birds

The occurrence of 138 distinct phrase types in the songs of 411 birds indicates that there is a great phrase variation—on the average, a different phrase for every third bird. In Ohio and Maine the variation was high in local areas. For example, Muscongus, Maine, had a different phrase type for almost every bird. This was higher than Maine—one phrase for every 3.45 birds. Yet Maine had less variation than the whole of New England and the Maritime Provinces which was one phrase for every 2.87 birds. This situation was also true for Ohio where the variation at Winous Point—2.00 birds per phrase—was greater than in all of Ohio—3.59—which in turn was less than the entire midwest—3.39 birds per phrase type.



Figures 84–104. Sonograms showing phrase similarities in the songs of different Yellowthroats: *Figures 84–85,* near Ithaca, New York: 84, type 4-35; 85, type 5-7. *Figures 86–87,* Hog Island, Lincoln County, Maine: 86, type 5-19; 87, type 5-17. *Figures 88–90,* Colorado: 88, type 3-49, Greeley; 89, type 3-57, Fort Morgan; 90, type 3-64, Masters. *Figures 91–93,* in Benton County, Oregon: 91, type 3-54; 92, type 3-58; 93, type 3-59. *Figures 94–97,* Hog Island, Lincoln County, Maine: 94–95, type 3-43; 96, type 4-24; 97, type 5-6. *Figures 98–104,* Clear Creek Valley, Hocking County, Ohio: 98, type 3-11; 99, type 3-16; 100, type 3-24; 101, type 3-40; 102, type 3-15; 103, type 3-46; 104, type 3-53.

TABLE 2

Incidence of Phrase Types in Yellowthroat Songs

Number of phrase types found in	*Number of phrase types*					
	2-noted	*3-noted*	*4-noted*	*5-noted*	*6-noted*	*Total*
1 bird	5	33	28	9	3	78
2 birds	1	7	5	4	1	18
3 birds	–	8	1	4	1	14
4 birds	–	4	1	–	–	5
5 birds	1	2	1	–	–	4
6 birds	–	2	1	–	–	3
8 birds	1	2	–	–	–	3
9 birds	–	2	–	–	–	2
10 birds	1	–	–	1	–	2
11 birds	–	1	–	–	–	1
13 birds	–	1	–	–	–	1
14 birds	–	1	–	–	–	1
16 birds	–	–	2	1	–	3
17 birds	–	1	–	–	–	1
18 birds	–	1	–	–	–	1
29 birds	–	1	–	–	–	1
1 subspecies	6	62	36	18	5	127
2 subspecies	2	4	3	1	–	10[1]
3 subspecies	1	–	–	–	–	1[2]
brachidactylus						
in 1 area[3]	5	46	27	13	1	92
in 2 areas[4]	1	4	3	–	–	8[3]

[1] *Brachidactylus* and *campicola,* 4 types (3–16, 3–26, 3–42, 4–24);
brachidactylus and *trichas,* 2 types (3–2, 2–1);
brachidactylus and *ignota,* 1 type (4–13);
trichas and *ignota,* 1 type (4–3);
typhicola and *ignota,* 1 type (5–3);
campicola and *scirpicola,* 1 type (2–8).

[2] *Brachidactylus, campicola,* and *occidentalis,* type 2–4.

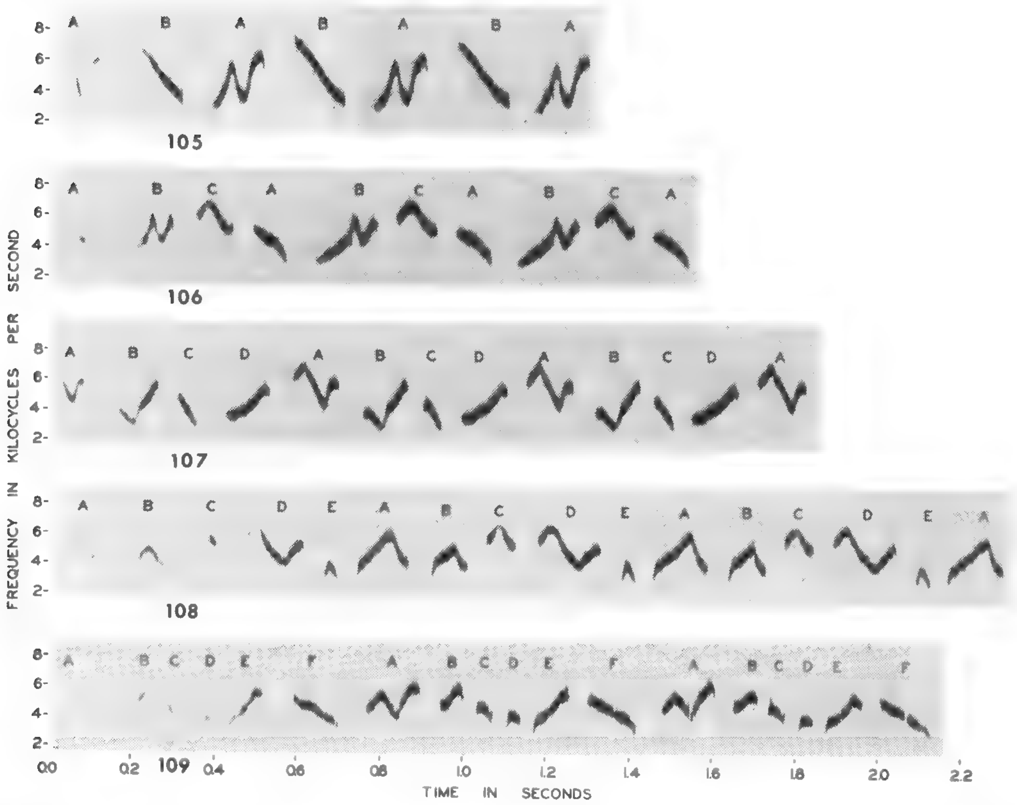
[3] In the three major northeastern areas.

[4] New England and midwest, 4 types (2—4, 3—8, 3—10, 3—11).
New York-Ontario and midwest, 4 types (3—16, 4—13, 4—32, 4—33).

By comparing the variation in the phrase types of the songs in areas represented by the same number of birds, the most separate of which are about the same distance apart, my data indicate a variation in different areas and also in the subspecies. For example, the song variation in local areas appears to be greater in the east than in either Colorado or Oregon. This is quite evident in the field. In Ohio or Maine, two birds with adjacent territories generally sang noticeably different phrases; in the western areas, two such birds often sang the same or very similar phrases. It appears that variation in the phrase types among birds of the subspecies *G. t. brachidactylus* (in the northeast) is greater than in *trichas* (mideastern) and in *ignota* (southeast) and that the variation in all three is greater than in *arizela* (far west).

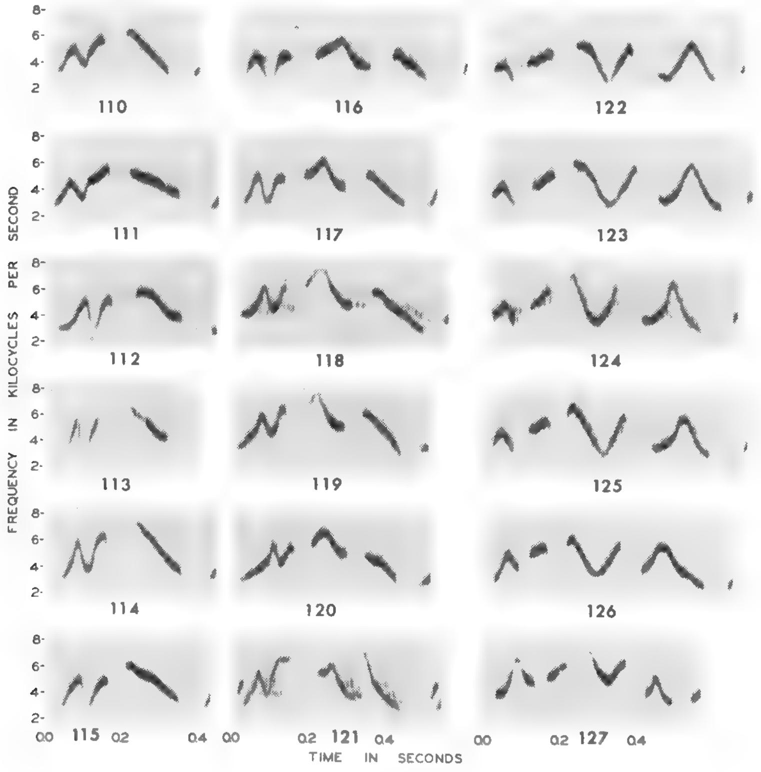
Geographic Range of Phrase Types

Individual phrase types are not confined to local areas and one phrase may extend over an entire state or a large section of it. Generally one phrase type did not occur over an entire section—e.g., the midwest.



Figures 105–109 (*Above*). Sonograms showing five Yellowthroat songs: 105, song with 2-note phrases, A–B–A–B–A–B–A, type 2-4, Greeley, Colorado; 106, 3-note phrases, A–B–C–A–B–C–A–B–C–A, type 3-26, Franklin County, Ohio; 107, 4-note phrases, A–B–C–D–A–B–C–D–A–B–C–D–A, type 4-14, Hog Island, Lincoln County, Maine; 108, 5-note phrases, A–B–C–D–E–A–B–C–D–E–A–B–C–D–E–A, type 5-17, Hog Island, Lincoln County, Maine; 109, 6-note phrases, A–B–C–D–E–F–A–B–C–D–E–F–A–B–C–D–E–F, type 6-4, Charleston, South Carolina.

Figures 110–127 (*Below*). Sonograms of Yellowthroat phrases showing variation within a phrase type. Figures 110–115, type 2-4: 110, Sur le Bateau, Quebec; 111, Albert Lea, Minnesota, 112, Kalamazoo, Michigan; 113, Lake Trois Cariboux, Quebec; 114, Greeley, Colorado; 115, Winous Point, Ottawa County, Ohio. Figures 116–121, type 3-26: 116, Buckeye Lake, Ohio; 117, Clear Creek Valley, Hocking County, Ohio; 118, Cranberry Glades, West Virginia; 119, Lexington, Virginia; 120, Franklin County, Ohio; 121, Jackson, Wyoming. Figures 122–127, type 4-24: 122–123, Hog Island, Lincoln County, Maine; 124, Nobleboro, Maine; 125, Medomak, Maine; 126, Hog Island, Lincoln County, Maine; 127, Delta, Manitoba.



Of the 138 different phrase types, 78 were sung by one bird each—and many were singing close to other recorded birds; the remaining 60 by from two to 29 birds each (Table 2). Ten of these phrase types were sung by two subspecies; one by three subspecies. The distance varied greatly—from the same phrase types sung by birds having adjacent territories to the same phrase types recorded 1,900 miles apart.

An average of the maximum distances between the most widely separated birds singing each of these 60 phrase types was about 282 miles. (In the case of borrowed recordings with inadequate data, I assumed that those taken in the same locality were from one to 20 miles apart.) If one includes zero miles apart for each of the 78 types sung by only one bird, the average is 123 miles. Therefore, one might safely say that a phrase type has a range of between 123 and 282 miles.

Variation within Phrase Types

In most Yellowthroat songs the first notes are relatively weak and show faintly on sonograms made with the instrument set low enough to avoid distortion of the louder notes. Thus, the first few notes in the sonograms (Figures 105–109) may appear to be a different type than those in the following phrases. Actually they are not different, but for clarity I have based my classification on the louder notes of the song.

Most songs showed minor variations from phrase to phrase in length, loudness of certain elements, and the like, but these variations were insignificant compared with the variations of the same song type from bird to bird. The songs of 13 birds definitely contained phrases of two or three different types.

Figures 110–127 illustrate some of the slight differences in phrases of a given type when sung by different birds.

1. Phrase Type 2–4 (Figures 110–115). No significant geographical trend. Quebec 110 was more like Minnesota 111 than like Quebec 113. Phrase length 0.34 second in Quebec 113 to 0.45 second in central Ohio.

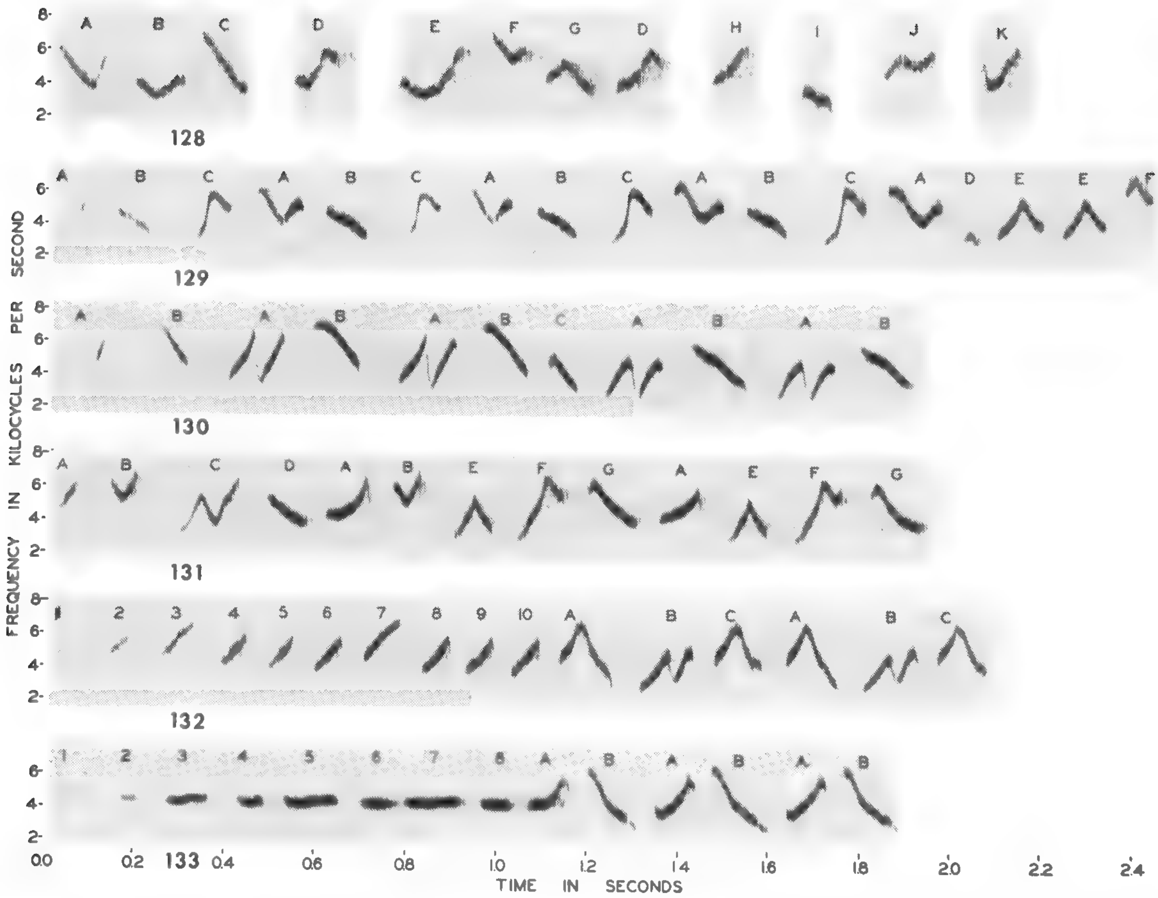
2. Phrase Type 3–26 (Figures 116–121). Marked variation between central Ohio 120 and northern Ohio 117 in length of first upslur of 3U note. Some birds in each area had the slur fairly long (central Ohio 120), while others had it shorter (northern Ohio 117). The slur was intermediate at distant points (West Virginia 118 and Virginia 119). Wyoming 121 manifested a little different phrase from that of the eastern birds (116–120). Phrase length 0.41 second in central Ohio 120 to 0.56 second in central Ohio 116, about 25 miles distant; 0.51 second in Wyoming 121.

3. Phrase Type 4–24 (Figures 122–127). All from Lincoln County, Maine except 127 from Manitoba. Some birds on Hog Island—122 and 123—had a distinct hook at the beginning of the last note of the phrase while others, Medomak 125, lacked it. Some had the downslur of the last note distinctly longer than the upslur (Hog Island 126). The birds on the mainland, near Hog Island—125 and 126—had phrases very similar to those on the island. Phrase length 0.56 to 0.68 second for birds in Maine; 0.53 second for Manitoba 127.

Geographic Variation

Form, Size, and Color

Behle (1950) made a detailed study of the geographic variation in the morphological characters in the western races of Yellowthroats. Two general



Figures 128–133. Sonograms of atypical Yellowthroat songs: 128, individual notes of the bird in Group 1, E–F–G–D, type 4-32. 129, Bird Number 4, Group 2, A–B–C–A–B–C–A–B–C–A–D–E–E–F, C–A–B, type 3-10 and A–D–E–E–F, type 5-14. 130, Bird Number 11, Group 2, A–B–A–B–A–B–C–A–B–A–B, A–B, type 2-4 and A–B–C, type 3-5. 131, Bird Number 6, Group 2, A–B–C–D–A–B–E–F–G–A–E–F–G, A–B–C, type 3-18, D–A–B–E, type 4-11, and F–G–A–E, type 4-12. 132, Ohio bird, Group 3, 1–2–3–4–5–6–7–8–9–10–A–B–C–A–B–C, A–B–C, type 3-47. 133, Minnesota bird, Group 3, 1–2–3–4–5–6–7–8–A–B–A–B–A–B, A–B, type 2-1.

aspects of this variation concern us here because of their similarity to the variation in song: (1) There is a great deal of individual variation in the form and structure in each race; individuals in the range of one race, even in the middle of the range, may have the characters of an adjacent or distant race; and the potentiality for all characters of form and structure seem to be present in all races to some degree. (2) Certain clines, or gradients in morphological characters, are evident in the western races of Yellowthroats and most of these progress independently, with each race showing a different combination of characters.

According to Behle (1950), the extent and intensity of the yellow of the underparts increase going southward; the back is darker in the west-coast races *arizela* and *sinuosa,* grayish green in the upper western plains *campicola,* yellower in southern west-coast *scirpicola,* and most yellowish in southwestern *chryseola.* The flank coloration is darker in coastal *arizela, sinuosa,* and *scirpicola,* and lighter in the interior races. The tail becomes longer going southward.

In the eastern birds (Sprunt, 1957), size increases slightly going northward from mideastern *trichas* to northeastern *brachidactylus.* Moving southward from *trichas* to southeastern *typhicola* and *ignota,* the tail and bill become longer, the yellow deeper, and the flanks darker. *Occidentalis,* a race rather widespread in western interior United States, is slightly larger than *trichas* with a longer tail, paler underparts, richer yellow beneath that extends farther back on the abdomen, and whiter edging of the face mask.

Song

Notes per Phrase (Tables 1 and 3). In the northeast (*brachidactylus*) there was a decrease in the average number of notes per phrase going westward. In the mideastern and southeastern parts of the United States (*trichas, typhicola,* and *ignota*) there was an increase in the average number of notes per phrase going southward. I found no geographic trends in notes per phrase in the western races. Six-note phrases occurred only along the east coast: one in *brachidactylus* in New Brunswick, three in *ignota* near Charleston, South Carolina, and four in *ignota* in Florida. Five-note phrases were found only in the four eastern races and were relatively rare in *brachidactylus* in the midwest. Four-note phrases occurred in one-fourth of the eastern birds and through most of the country except in *occidentalis, chryseola,* or *arizela.* The incidence of four-note phrases decreased going westward. Three-note phrases were found in every race except *sinuosa* in the far west. Three-note phrases were sung by a little less than one-third of the birds in New England and the Maritime Provinces, and their incidence increased going westward and decreased going southward.

In studying notes-per-phrase, let us consider one area in south-central Maine where I recorded 90 birds singing 3-note, 4-note, and 5-note phrases. I made 45 recordings on islands, 100 yards to 8 miles offshore, and 44 on the adjacent mainland, 25 yards to 20 miles from the coast. About the same number in each group (17 island and 21 mainland) sang the 4-note phrase, but the proportion was different with the 3-note and 5-note phrase. The island birds sang three times as many 5-note phrases and only about half as many 3-note phrases as the mainland birds.

TABLE 3

Data on Note and Phrase Complexity in Yellowthroat Songs

(Averages plus or minus the standard error)

Area and subspecies	*Notes per phrase*	*Elements per phrase*	*Elements per note*
Northeastern: *brachidactylus*			
Northern England and Maritimes	4.00 ± 0.08	7.57 ± 0.19	1.89 ± 0.03
New York and Ontario	3.76 ± 0.13	7.68 ± 0.26	2.04 ± 0.09
Midwestern	3.05 ± 0.03	5.74 ± 0.09	1.88 ± 0.03
Total	3.44 ± 0.04	6.53 ± 0.10	1.90 ± 0.02
Mideastern			
trichas	3.38 ± 0.29	5.67 ± 0.44	1.68 ± 0.13
typhicola	4.50 ± 0.50	6.00	1.33 ± 0.24
Total	3.48 ± 0.27	5.70 ± 0.40	1.64 ± 0.12
Southeastern: *ignota*	4.89 ± 0.25	7.44 ± 0.24	1.52 ± 0.09
Western Plains			
campicola	3.00 ± 0.24	6.33 ± 0.37	2.11 ± 0.17
occidentalis	2.89 ± 0.08	8.00 ± 0.45	2.77 ± 0.14
chryseola	3.00	8.50 ± 0.50	2.83 ± 0.27
Total	2.94 ± 0.08	7.58 ± 0.32	2.58 ± 0.10
Far West			
arizela	2.90 ± 0.10	8.40 ± 0.27	2.90 ± 0.20
sinuosa	4.00	8.00	2.00 ± 0.71
scirpicola	3.00 ± 0.58	8.33 ± 1.45	2.78 ± 0.70
Total	3.00 ± 0.15	8.36 ± 0.32	2.79 ± 0.24
All Birds	3.45 ± 0.04	6.66 ± 0.09	1.93 ± 0.02

Note and Phrase Complexity (Table 3). Note complexity, the number of elements per note, was greater in western than in eastern birds. In the east there was a decreasing complexity going south; in the western plains there was an increasing complexity going south; in the far west no significant trends in note complexity were evident.

Phrase complexity, the number of elements per phrase, showed a slight decrease westward in *brachidactylus;* it was a little less in *trichas* and *typhicola;* and increased again farther south in *ignota.* The phrases of most of the western races were more complex than the eastern; and in the western plains there was an indication of an increasing complexity going south.

TABLE 4

Occurrence of Note Types in Yellowthroat Songs

(Figures in per cent to nearest whole number)

Area and subspecies	*Note type*											
	1U	1D	2U	2D	3U	3D	4U	4D	5U	5D	U	D
Northeastern:												
brachidactylus												
New England, Maritimes	16	11	40	17	12	2	0	0	1	0	70	31
New York and Ontario	5	20	44	12	7	2	2	6	0	1	59	41
Midwestern	9	26	29	15	15	3	1	2	0	0	53	47
Total	12	20	35	16	13	3	1	2	0	1	60	40
Mideastern:												
trichas	30	38	7	1	13	0	0	11	0	0	49	51
typhicola	44	33	11	0	11	0	0	0	0	0	67	33
Total	31	38	8	1	13	0	0	10	0	0	51	49
Southeastern:												
ignota	33	33	11	7	14	0	0	2	0	0	58	42
Western Plains:												
campicola	4	19	44	7	15	7	0	0	4	0	67	33
occidentalis	0	4	40	0	21	21	2	0	12	0	75	25
chryseola	0	8	25	0	33	8	25	0	0	0	83	17
Total	1	9	40	2	21	15	4	0	8	0	74	26
Far West:												
arizela	7	0	41	3	7	7	17	3	10	3	83	17
sinuosa	0	50	25	0	0	0	0	25	0	0	25	75
scirpicola	11	44	0	0	0	0	0	0	44	0	56	44
Total	7	14	31	2	5	5	12	5	17	2	71	29
All Birds	13	21	32	13	13	3	1	2	1	0	61	39

Note Types (Table 4). Notes consisting of a single element, 1U and 1D, comprised nearly a third of the notes of the northeastern birds and about two-thirds of those in mideastern and southeastern birds, but were relatively uncommon in western birds, except *sinuosa* and *scirpicola* in the far west. Notes with two elements made up 45 per cent, or nearly half, of all the notes studied. Their occurrence was highest in the northeast, significantly lower in the mideast and southeast, and slightly lower in the southwest. Notes with three elements were most common on the western plains where they made up about one-third of the notes. They did not occur in *sinuosa* or *scirpicola.* Notes with four or five elements were common only in the far west where together they made up over one-third of the notes.

Phrase Length. On the average, and in nearly all areas, the length of the phrase increased with the number of notes per phrase. For example, in the northeastern birds (*brachidactylus*) the average length of a 2-note phrase was 0.3 second, while that of a 6-note phrase was 0.7 second. Two-note phrases increased in average length going westward from 0.3 second in the northeast to 0.5 second in the far west. Three- and 4-note phrases were a little shorter in the northeast than elsewhere, but no geographic trend was evident. Considering all phrases, there was a slight decrease in length from 0.6 second in the northeast to 0.5 second in the far west, and the longest phrases were in the southeast (*ignota*) with an average of 0.7 second. This may reflect the corresponding increase in the average number of notes per phrase in the southeastern birds.

The variation in song parallels to some extent the variation in morphological characters. The song trends going southward in the east show: (1) an increase in phrase length, (2) an increase in the number of notes per phrase, and (3) a decrease in number of elements per note. This parallels the morphological trends toward deepening yellow below, darkening flanks, and the longer tail and bill. Song trends from north to south in the western plains show an increase in the number of elements per note and elements per phrase. This parallels the increasing intensity and extent of the yellow underparts of the birds. While there is a morphological cline of deepening yellow of the underparts in both eastern and western birds going southward, the trend in note complexity in the east is toward a decrease and in the west toward an increase. Some clines in song variation, especially those in *brachidactylus*, do not parallel any known cline in morphological characters. In local populations there is considerable variation in song, just as in morphological characters, and individual birds in the middle of the range of one race may have a phrase or type of note very similar or identical to that of another race.

Atypical Songs

The songs of 16 of the 411 birds, which did not fit the pattern of from two to five similar phrases each, were considered atypical and divided into three groups:

Group 1. Phrasing variable from song to song and considerable variation in individual notes (1 bird).

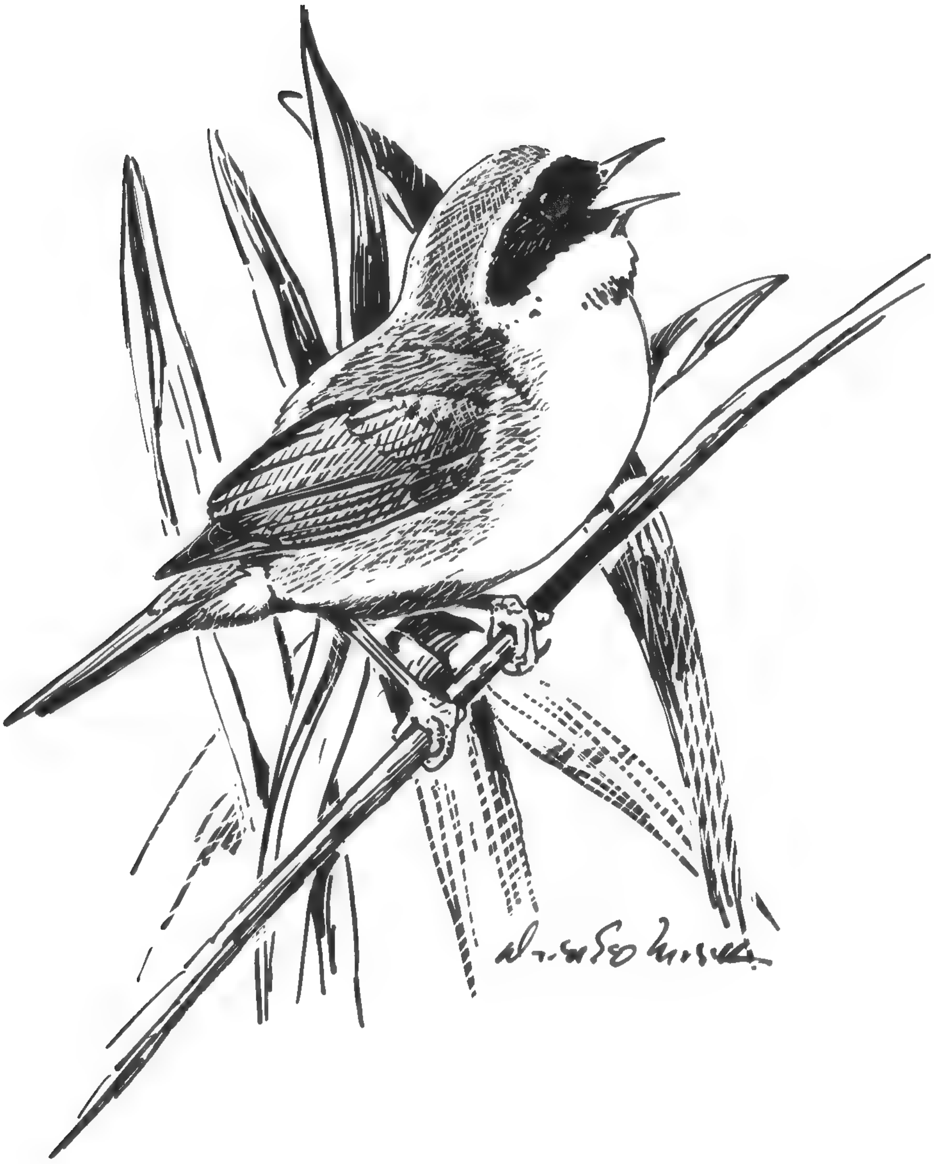
Group 2. Two or three phrase types in each song (13 birds).

Group 3. Beginning with a series of 6 to 10 similar notes and ending with a series of typical multiple-note phrases.

Ordinarily, the atypical songs of passerine birds fall into four general categories: (1) The specialized songs, heard infrequently, such as whisper songs or songs during flight or courtship. (2) Subsongs representing a stage in the development of song in the individual bird toward the definitive advertising songs. (3) Songs representing aberrant versions of the normal song of the species. (4) Songs influenced by and consequently mimicking those of another species.

Group 1

Represented by one bird (OSU 7556, 25 songs, Blendon Woods, Franklin County, Ohio, 18 May 1965) which sang at a somewhat irregular rate and frequently scolded between songs. The 25 songs included 11 different notes



Yellowthroat. Drawing by Donald Leo Malick.

(see Figure 128, A-K and Table 5). One sequence of notes (E-F-G-D, Figure 128, Phrase Type 4–32) occurred at least once in 24 of the songs and, in many, more than once. Most songs began with various note combinations and many ended with odd combinations.

This recording probably represents subsong. The bird appeared to have difficulty getting the song into its definitive phrase type and holding this phrase to the end. Presumably, as the bird continues singing, the notes and phrases will become more uniform and the odd notes will be dropped or modified to the notes of the definitive phrase, E, F, G, and D. Unfortunately, I was unable to check this bird's progress by making recordings at a later date.

The period of subsong in this species may be relatively short. Of my 375 recordings, made from March in the south to midsummer in the north, this is the only one that appears to represent a subsong.

TABLE 5

Note Composition of the 25 Songs of Yellowthroat Recording 7556

							Phrase 4–30[1]							
Song 1	F	A	B	C	D	E	F	G	D	E				
Song 2			A	E	A	E	F	G	D	E	F	G		
Song 3				E	A	E	F	G	D	E	C			
Song 4		A	E	C	D	E	F	G	D					
Song 5		A	E	C	D	E	F	G	D	E	F			
Song 6					A	E	F	G	D	E	F	G	D	E
Song 7				A	J	E	F	G	D	E	F	G	D	
Song 8					A	E	F	H	D	C	D	E		
Song 9			A	G	D	E	F	G	D	E	F	G		
Song 10					A	E	F	G	D	E	F	G	D	E
Song 11				E	A	E	F	G	D	E	F	G		
Song 12			C	E	A	E	F	G	D	E				
Song 13		C	D	E	A	E	F	G	D	E				
Song 14					A	E	F	G	D	E	F	D	D	E
Song 15					A	E	F	G	D	E	F	G	D	E
Song 16		A	E	C	D	E	F	G	D	I	K	A		
Song 17					A	E	F	G	D	E	F	G	D	K
Song 18				G	D	E	F	G	D	E	F	G	D	
Song 19					A	E	F	G	D	E	F	G	D	E
Song 20					K	E	F	G	D	E	F	G	D	E
Song 21					A	E	F	G	D	E	F	E	F	G
Song 22		A	E	C	D	E	F	G	D	E				
Song 23				A	H	E	F	G	D	E	F	G		
Song 24		A	E	C	D	E	F	G	D	E				
Song 25				C	D	E	F	G	D	E	C			

[1]Except in Song 8.

Group 2

Songs of 13 birds (12 *brachidactylus* and 1 *scirpicola*) contained two or three phrase types:

Locale	*Phrase types*
Maine	
1. Hog Island, Lincoln County	4–14, 5–14
2. Hog Island, Lincoln County	3–10, 4–21
3. Hog Island, Lincoln County	5–17, 5–19
4. Hog Island, Lincoln County	3–10, 5–14
5. Lincoln County	3–11, 4–24, 5–6
6. Keene Neck, Lincoln County	3–18, 4–11, 4–12
Vermont	
7. East Brookfield	3–31, 3–19
Ohio	
8. Blendon Woods, Franklin County	3–16, 4–29
9. Blacklick Woods, Franklin County	3–24, 3–26
10. Winous Point, Ottawa County	2–4, 3–5
11. Mansfield	3–11, 3–44
12. Delaware County	3–8, 3–10
California	
13. Southern part	2–8, 3–66

In these songs I find it hard to decide just which notes constitute each phrase. For example, the song of Hog Island Bird Number 4 (see Figure 129) contained 14 notes: A-B-C-A-B-C-A-B-C-A-D-E-E-F. The first phrase, Type 3–10 and obviously A-B-C, B-C-A, or C-A-B, was recorded from two atypical birds on Hog Island and 16 typical birds in Maine and central Ohio. The second phrase type is not so clear. It might be C-A-D-E-E-F, A-D-E-E-F, or D-E-E-F. I believe it is A-D-E-E-F because I found this same type in the song of Bird Number 2 on Hog Island and I did not find any phrases resembling the other two in any songs.

Most phrases of the birds with two or three phrase types had one or more notes the same: The two phrase types, sung by four birds, were alike except that one type contained an additional note; the notes of two birds with three-note phrases were the same except that the third note was different; six birds had two or more notes different; one bird had all the notes of the two phrase types different.

The songs of each of eight birds in Group 2 were essentially the same, the only significant variation being in the number of phrases of each type. The songs of four other birds varied similarly, but one or two songs of each recording contained only phrases of the first type. One song of Bird Number 6 (usual song Figure 131) contained only a phrase of the first type, A-B-C, and part of the second, D-A-B-E, with nothing of the last, F-G-A-E. One song of Number 8 contained four phrases—Types 3–16, 4–29, 3–16, 4–29.

I recorded all of the songs in Group 2 except that from California and the birds all appeared to be singing the advertising song. Except for Bird Number 8, recorded on 8 May, the season was much too late for subsong.

The songs in Group 2 are probably aberrant versions of the species' normal songs, Category 3. Except for Number 13 which I did not record and Number 8, recorded on 5 May, I believe they were all singing the advertising song. Number 8 could have been a subsong.

Group 3

The songs of two birds (OSU 1047, 11 songs, Columbus, Ohio, 19 May 1954; Cornell Cut 57, 9 songs, Ely, Minnesota, 18 June 1963) began with a series of six to 10 similar notes and ended with a series of typical multiple-note phrases (Figures 132 and 133).

Each recording differed only in the number of introductory notes and/or the number of final phrases. Four songs of the Ohio bird (Figure 132) began with six abruptly upslurred notes and seven songs began with 10 abruptly upslurred notes and ended with two, or two and two-thirds, 3-note phrases (Type 3–47). The songs of the Minnesota bird (Figure 133) began with from six to 10 short notes of uniform pitch, but of slightly varying length, and ended with from three to five 2-note phrases (Type 2–1). The Ohio bird sang from low bushes in a river bottom, the Minnesota bird from a spruce bog.

In some respects these songs resemble the flight-song (Saunders, 1935:211) except that Saunders indicates that the pitch of the introductory notes of the flight-song varies considerably, and the birds were not in flight when the songs were recorded. Although I cannot say positively that the Ohio bird was not singing a courtship or an aggressive song, I saw no other Yellowthroat in the vicinity at the time. Perhaps these two songs belong in Category 4, and the unusual notes may have developed under the influence of another species—possibly a Field Sparrow (*Spizella pusilla*).

Birds with Similar Songs

A number of other passerines have songs of a series of similar phrases that resemble the songs of the Yellowthroat. The Carolina Wren (*Thryothorus ludovicianus*), Ovenbird (*Seiurus aurocapillus*), Kentucky Warbler (*Oporornis formosus*), and Connecticut Warbler (*Oporornis agilis*) are probably the closest.

In songs of the Carolina Wren (Borror, 1956) there is variation in the number and length of the phrases, and only the shorter, slower songs are likely to be confused with Yellowthroat songs. The chief difference lies in the quality of the songs and the birds' singing habits. The wren sings faster and has a vocabulary of several phrase types, using one type for a while and then changing to another.

The songs of the Ovenbird and Kentucky Warbler generally contain more than five phrases; the separation between phrases is longer than in the song of the Yellowthroat, and the birds sing only about three songs a minute. The Yellowthroat sings four or five a minute. Ovenbird songs regularly contain short, very abruptly slurred elements (rare or absent in Yellowthroat songs). The songs of the Kentucky Warbler are lower pitched.

The songs of the Connecticut Warbler, similar to Yellowthroat songs in note rate, notes per phrase, phrase rate, and phrases in the song, contain abruptly slurred elements that give the songs a more staccato quality than those of the Yellowthroat. The Connecticut Warbler songs are also a little lower in pitch.

Phrase Acquisition by the Individual Bird

The question arises as to how a particular Yellowthroat happens to sing its one particular phrase. Field data, although they cannot answer this, may suggest the factors involved. The species-specific features of the songs are probably inherited; the differences in different birds or populations of birds may be due to genetic variations, learning, or chance.

TABLE 6

Occurrence of Phrase Types in Yellowthroat Songs
at Hog Island, Lincoln County, Maine

Phrase types	*Year*			
	1959	*1960*	*1961*	*1962*
3–8			+	
3–10	+		+	
3–43		+	+	+
4–14		+	+	+
4–21	+			
4–24	+	+	+	+
5–6	+	+	+	+
5–14			+	
5–15			+	
5–16	+	+		+
5–17	+	+	+	+
5–19	+			
Number of birds	7	7	10	8
Number of phrase types	7	6	9	6

The one recording that appeared to be a subsong suggests that the songs of a given bird, starting with a variety of note types and arrangements, may eventually settle on a particular sequence of particular notes. The types of notes are probably hereditary; the phrase type developed might be by chance, by learning, or a combination of factors.

The field recording alone cannot determine whether the similarities in song in a local population are hereditary (drawn from a common gene pool) or learned. The amount of variation differs from one local population to another (more variation in eastern populations than in western). Does this reflect a difference in the size of the gene pools or a difference in learning?

Let us consider the role of chance. There are four possible 3-note sequences of 1- and 2-element notes: 1-1-1, 1-1-2, 1-2-2, and 2-2-2. If it were a matter of chance as to which was sung by a given bird, each sequence would be sung by an equal number of birds. But that did not happen. Of the 69 *brachidactylus* individuals singing such 3-note phrases, none sang 1-1-1, 14 sang 1-1-2, 52 sang 1-2-2, and three sang 2-2-2. The same situation occurred in the upslur and downslur notes. Chance may play some slight role in phrase acquisition but learning and heredity must also be involved.

It seems probable — at least in the east where there is greater variation within local populations—that heredity is more important in phrase acquisition. Table 6 lists the phrase types sung by birds on 30-acre Hog Island in Maine during four successive seasons in which I believe I recorded every male present. Each season almost every bird sang a different phrase, and the phrases occurring were not the same in any two successive seasons. Only three phrase types (4–24, 5–6, 5–17) occurred in each of the four seasons. Some of the birds in the area (those singing 4–24, 5–6, 5–17) might have learned their phrases by hearing nearby birds. Others (those with 3–8, 5–14, 5–15) probably did not. Although learning may play a partial role in the acquisition of a phrase type, it does not appear to be the sole mechanism involved.

Differences between phrases can come about by changes in notes—the loss or addition of elements, the separation of elements, or the combining of elements. Just how such changes happen—whether by chance in one individual and by mimicry in another, or by mutation—there is no positive answer.

Changes in Yellowthroat Songs Over the Years

The evidence of a change in Yellowthroat songs over the years is similar to that cited in Borror and Gunn (1965) for the White-throated Sparrow (*Zonotrichia albicollis*). Mathews (1921:201) states that "all the Maryland Yellowthroats around Boston and also the White Mountain region sing a trisyllabic song," and he mentions hearing songs of 4-note phrases only once—from a bird near New York. Since Mathews' book is a revision of one published in 1904, it is probable that most of the observations on which his statement is based were made 60 or more years ago.

The Yellowthroat recordings that I studied included two from New Hampshire (one 4-note phrase, 1954; one 3-note phrase, 1962), none from Massachusetts, 101 from Maine, four from Vermont, and 18 from New York. Most recordings were made from 1953 to 1963; the oldest, from Ithaca, New York, 1947 and 1948, contain 4-note phrases.

I found 3-note phrases in the songs of only 31.5 per cent of the birds in New England and the Maritime Provinces, and in 36 per cent in New York and Ontario. I found the 4-note phrase in 37.8 per cent of New England birds and 52 per cent of New York and Ontario birds, and the 5-note phrase in 33.3 and 12 per cent of the birds in these two areas (Table 1). This indicates that only about a third of the Yellowthroats in the northeast have been singing 3-note phrases in the last 15 or 20 years, and about two-thirds of them have been singing 4- and 5-note phrases.

We may assume, from the detail he shows in the songs of other birds, that, although Mathews had no electronic equipment, he was able to distinguish between 3-, 4-, and 5-note phrases, and that the birds around Boston and in New Hampshire were not singing 4- and 5-note phrases 60 years ago. The predominance of 4- and 5-note phrases in the songs of New England birds at the present time indicates that the average number of notes per phrase has increased in the last 60 years.

Summary

This paper, based on a study of the recorded songs of 411 Yellowthroats (*Geothlypis trichas*) representing 10 North American subspecies, is concerned with the nature and extent of the variation in the advertising songs of the Yellowthroat and the implications in this variation.

A Yellowthroat song consists of from two to five repetitions of a sequence of notes known as a phrase. Each note consists of from one to five slurred elements. I classified the recordings into 138 phrase types, each containing from two to six notes.

The songs of a given individual varied little except in length. The phrases of different birds showed considerable variation with about every third bird singing a different phrase. The variation in a local area in eastern North America was generally greater than that found in the larger area of which the small one was a part. There was greater variation among local populations in the east than in the west.

Sixty of the 138 phrase types were sung by from two to 29 birds; one of these was sung by individuals of three subspecies, 10 by individuals of two subspecies, and the rest by individuals of one subspecies. The distance separating birds singing the same phrase varied from nothing, on adjacent territories, to 1,900 miles; half of the 60 were sung by birds 50 or more miles apart. Some phrases are common; others quite rare.

I found geographic variation in number of notes per phrase, complexity of notes and phrases, and length of phrases. In the northeast (*G. t. brachidactylus*), the average number of notes per phrase and the phrase length decreased going from east to west. Six-note phrases occurred only along the east coast; 5-note phrases only as far west as Ohio. In the east, going from north to south, there was a trend toward increasing phrase length and the number of notes per phrase, and a decreasing number of elements per note (complexity). The complexity of notes averaged higher in western birds than in eastern, and, in the western plains, tended to increase going southward. Some of the geographic variation in song paralleled clines in morphological variation; others did not.

Sixteen of the 411 birds sang atypical songs. Of these songs one was irregular at the beginning and end; 13 contained two or three phrase types each; and two began with a series of six to 10 similar notes and ended with typical multiple-note phrases.

The principal species-specific features of Yellowthroat songs are their form, quality, and the singing habits of the birds. The songs of other species, similar to those of the Yellowthroat, differ from them in phrase rate, number of phrases, distinctness of phrases, quality, singing rate, and/or number of phrase types.

The species-specific features of the Yellowthroat song are probably hereditary with variations resulting from genetic variation, learning, and/or chance. Evidence from field recordings suggests that heredity probably plays a significant role in phrase acquisition — in the type of notes and, possibly to some extent, the phrases — and that learning and chance play only minor roles.

Descriptions of songs of Yellowthroats in New England some 60 years ago show that these birds then sang almost exclusively 3-note phrases. According to my recordings about two-thirds of the New England birds now sing 4- and 5-note phrases. This indicates that in the last 60 years the average number of notes per phrase has increased in this region.

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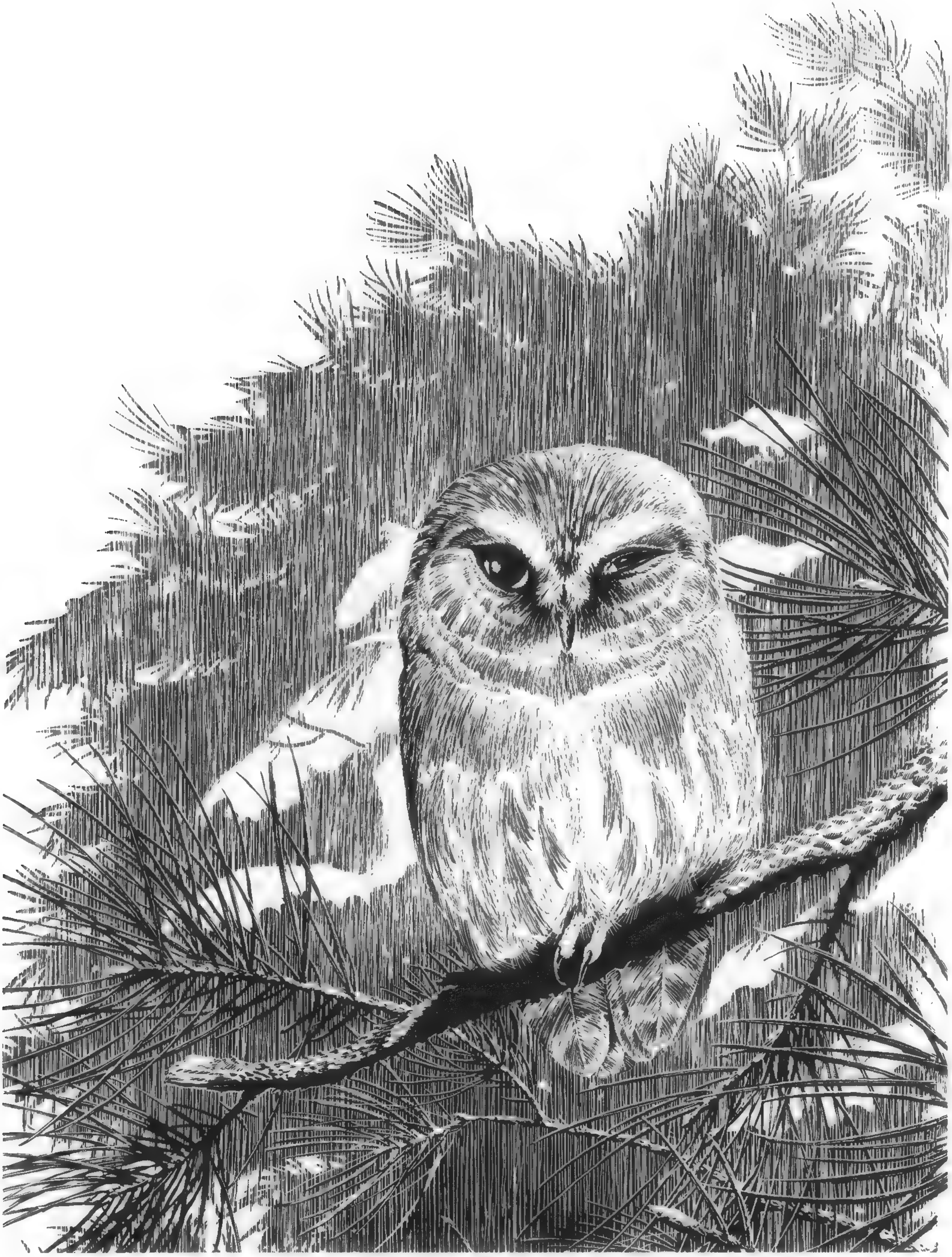

Saw-whet Owl, *Aegolius acadicus*. Drawing by John R. Quinn.

THE STATUS OF NEWELL'S RACE OF THE MANX SHEARWATER[1]

WARREN B. KING AND PATRICK J. GOULD

The Manx Shearwater (*Puffinus puffinus*) is an oceanic superspecies distributed around the world in the subtropical and temperate climatic zones. Murphy (1952) divided the group into eight largely allopatric races of which *P. p. newelli* Henshaw in the north-central Pacific Ocean is one. W. R. P. Bourne (*in* Palmer, 1962) placed *newelli* in a subgroup with *P. p. puffinus, yelkouan,* and *auricularis,* which comprises the dark- or black-backed, cool water form rather than the brown-backed form.

The race *newelli,* which we will refer to in this paper as Newell's Shearwater, is distinguished from the other black-backed races by the relative lack of dark feathers speckling the sides of the neck, causing the line of demarcation between upperparts and underparts to be sharper, less diffused. It is further distinguished from *auricularis,* with which there might be a range overlap at sea, by having mainly white undertail coverts, whereas *auricularis* has mainly black undertail coverts. In the field the black upperparts of Newell's Shearwater and contrasting white underparts set it apart from other central Pacific shearwaters and petrels (see Plate 1). Its underwings — an important field character in the shearwaters — are white with thin black leading margins. Prominent white feather-patches extend dorsally behind the wings into the sides of the lower back and rump. Its flight, a series of rapid wing-beats on stiff wings interspersed with short glides, is characteristic of other races of the Manx Shearwater as well.

We know less about *newelli* than any of the other populations of the Manx Shearwater. No authenticated record of this race was ever obtained between 1894, when the type specimen was taken, and 1954, when a bird was collected on Oahu, Hawaiian Islands (Richardson, 1955). During this period the race was thought to be extinct, or nearly so (Peters, 1931), although unconfirmed reports of birds, seen at sea and presumed to be Newell's Shearwaters, indicated the continued existence of at least a small population (Munro, 1941, and Fisher, 1951).

In recent years Newell's Shearwater, its status still unknown or in doubt (IUCN, 1966; U.S. Department of Interior Committee on Rare and Endangered Wildlife Species, 1966; Greenway, 1958), has been considered either rare or in danger of extinction.

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[1] Paper Number 29, Pacific Ocean Biological Survey Program.

This paper summarizes data gathered on Newell's Shearwater by the Smithsonian Institution's Pacific Ocean Biological Survey Program from 1963 to the present. We have included additional information from other sources, some previously unreported, in order to present as complete and clear a picture as possible of the bird's status.

We are grateful to the authorities of the Auckland Institute and Museum, Auckland, New Zealand (AIM), the Dominion Museum, Wellington, New Zealand (DMNZ), the American Museum of Natural History, New York (AMNH), the Peabody Museum of Natural History, New Haven (YPM), Bernice P. Bishop Museum, Honolulu (BPBM), and the Kokee Natural History Museum, Kokee, Kauai (KM) for loaning specimens or permitting us to examine their collections.

Specimen Records

A lack of specimen material has left the systematic status of Newell's Shearwater unresolved. Although eight specimens were taken before 1895, Murphy (1952) could locate only two, the type (BPBM 4292) and another (BPBM 1100), one of four in the Gay and Robinson collection, taken by Francis Gay on Kauai before 1891 (see Table 1).

The type specimen was taken in Waihee Valley, Maui, in 1894 by natives who turned it and several others over to Brother Matthias Newell, a Catholic missionary on Maui. Brother Matthias preserved two as specimens, one of which he gave to H. W. Henshaw, a prominent ornithologist in Hawaii. Henshaw (1900) described the specimen as a new species and at a later date presented it to the Bishop Museum in Honolulu. The other was in the St. Louis College (now Chaminade College), Honolulu, collection which was given to the Bishop Museum in 1966 after specimens in bad repair were thrown away. Brother Matthias' second specimen was evidently discarded.

Francis Gay gave the four Gay and Robinson birds to the Bishop Museum in 1900. W. A. Bryan had in manuscript a description of the second of these four, BPBM 9307, when Henshaw's publication appeared. Bryan (1901) published his description anyway, and acknowledged the name (*Puffinus newelli*), given by Henshaw, rather than naming it after Francis Gay as he had intended. Specimen BPBM 9307 has disappeared. It is not in the Bishop Museum.

A third specimen from the Gay and Robinson collection, now in the Auckland Museum, Auckland, New Zealand (unnumbered), is dateless, but the collector is listed as F. Gay. The location of the fourth specimen is still unknown.

The seventh specimen known prior to 1954 was taken on the summit of the mountain between Pelekunu and Waikolu Valleys on Molokai and belonged to a Mrs. Wilson who lived in Pelekunu Valley, Molokai (Bryan, 1908). We have not attempted to locate this specimen.

The oldest specimen, collected on Saipan, Marianas, by Marché in May 1887 (Jouanin, 1956), was originally identified as *Puffinus obscurus* by Oustalet (1896), who thought it larger, blacker above, contrasting more sharply with the white underparts than *"P. obscurus"* (=*P. lherminieri bailloni*) seen in the Seychelles. Jouanin at the Paris Museum of Natural History recently reidentified it (Paris Museum Specimen 5099). Oustalet's statement that this bird was a well-known breeding species on Saipan referred to *P. lherminieri dichrous* which is now known to breed there (Baker, 1951).

Between 1954 and 1961 seven new specimens were taken (Table 2). Three of these are previously unreported.

TABLE 1
Specimens of Newell's Shearwater Taken prior to 1900

Museum and Number	*Date*	*Collector*	*Locality*	*Sex*	*Wing*	*Tail*	*Culmen*	*Tarsus*	*Middle toe and claw*
Paris 5099	May 1887	M. Marché	Saipan, Marianas	F	247	84	33	47	50.5
BPBM 1100	Before 1891	F. Gay	Kauai	—	241	84	33.5	47	51.6
AIM Unnumbered	Before 1891	F. Gay	Kauai	—	240	82.0	30.5	43.7	48.7
BPBM 9307 (lost)	Before 1891	F. Gay	Kauai						
Lost	Before 1891	F. Gay	Kauai?						
BPBM 4292	Spring 1894	M. Newell	Waihee Valley, Maui	—	221 (molt)	76 (molt)	33.0	47	47
St. Louis College (destroyed) 1966	Spring 1894	M. Newell	Waihee Valley, Maui	—					
?	?	Mrs. Wilson	Pelekunu, Molokai						

TABLE 2
Specimens of Newell's Shearwater Taken between 1954 and 1961

Museum and Number	*Date*	*Collector*	*Locality*	*Sex*	*Wing*	*Tail*	*Culmen*	*Tarsus*	*Middle toe and claw*
AMNH 468, 881	22 May 1954	F. Richardson (1955)	Aiea, Oahu	F	231	79.9	31.7	45.4	51.0
DMNZ 9576	11 May 1956	G. C. Munro (unreported)	Hawaiian Islands	M	233	85.3	32.8	47.5	54.3
YPM 36, 952	8 October 1956	G. C. Munro (*in* Ripley, 1957)	Koloa, Kauai	M	233	79.3	32.9	47.5	48.1
YPM 7573	5 November 1956	J. Bowles (unreported)	Kilauea, Kauai	?	240	82.8	34.0	46.0	52.5
KM Unnumbered	? October 1957?	Hui O Laka (*in* Hadley, 1961)	Kauai						
BPBM 6692	31 July 1960	(unreported)	Wailua, Kauai	?	243	85.0	35.0	48.0	
BPBM 6707	3 July 1961	J. Bowles (1962)	Honolulu, Oahu	F	235	85.0	32.5	47.5	

TABLE 3

Specimens of Newell's Shearwater at the Smithsonian Institution

U.S. National Museum Number	*Date*	*Collector*	*Locality*	*Sex*	*Wing*	*Tail*	*Culmen*	*Tarsus*	*Middle toe and claw*	*Weight*
492973	21 August 1963	A. B. Amerson	Sand Island, Johnston Atoll	F	244	85.5	33.3	45.6	52.4	
493644	5 June 1964	L. N. Huber	6°51′N, 161°36′W	F	227	85.1	34.1	45.4	48.4	
493645	6 July 1964	C. B. Kepler	11°34′N, 170°43′W	F	240	87.9	33.5	44.4	46.8	342.5
493646	8 July 1964	W. B. King	Hanalei Plantation Hotel, Kauai	F	233	82.9	33.6	45.5	45.6	
493647	5 September 1964	K. E. Amerman	19°41′N, 162°05′W	F	240	85.2	31.0	47.1	48.0	398
494187	25 September 1964	G. E. Swedberg	Kauai	F	228	80.7	30.6	45.2	46.4	
494183	25 October 1964	W. B. King	Lihue, Kauai	F	228	83.0	32.6	44.4	46.7	
494185	25 October 1964	D. A. Bratley	Hanapepe, Kauai	F	234	82.6	31.0	44.9	47.1	
494180	29 October 1964	W. B. King	Kilauea Point, Kauai	?	226	81.8	31.3	43.7	47.3	
494190	29 October 1964	W. B. King	Kilauea Point, Kauai	?	243	77.1 (worn)	34.3	47.3	48.7	
494188	30 October 1964	W. B. King	Wailua, Kauai	M	241	85.4	32.4	45.2	51.2	
494181	October 1964	G. E. Swedberg	Kauai	M	223	85.5	32.6	43.9	48.1	
494182	October 1964	G. E. Swedberg	Kauai	?	239	78.9	33.3	45.7	46.2	
494184	October 1964	G. E. Swedberg	Kauai	M	201 (molt)	77.9 (molt)	32.3	44.9	47.3	
494186	October 1964	G. E. Swedberg	Kauai	M	232	79.5	34.0	44.7	48.2	
494189	October 1964	G. E. Swedberg	Kauai	?	242	79.9	34.4	45.6	46.2	
495848	4 May 1965	W. B. King	Kilauea Point, Kauai	F	235	84.9	33.4	46.9	49.1	
495849	4 May 1965	W. B. King	Kilauea Point, Kauai	?	238	85.6	34.8	45.3	53.6	
495850	4 May 1965	W. B. King	Kilauea Point, Kauai	M	245	86.4	35.5	45.4	52.0	
495847	6 May 1965	W. B. King	Kauai	F	238	85.5	33.4	47.2	49.9	397
495240	24 May 1965	D. N. Husted	21°44′N, 161°11′W	M	244	87.6	33.4	46.3	49.0	424
495241	8 June 1965	D. N. Husted	10°41′N, 149°16′W	M	239	83.5	32.5	47.2	50.2	390
495640	24 June 1965	B. A. Harrington	20°36′N, 160°05′W	M	245	88.8	35.0	43.3	48.3	389
496325	3 February 1966	R. S. Crossin	06°22′N, 174°20′W	F	238	85.5	33.5	47.2	48.5	408
496561	15 June 1966	L. N. Huber	Kuku Point, Wilkes I., Wake I.	F	249	87.9	33.5	48.3	51.4	
496562	15 June 1966	L. N. Huber	Kuku Point, Wilkes I., Wake I.	F	245	88.7	34.2	45.8	49.4	
496516	25 June 1966	R. S. Crossin	21°56′N, 159°46′W	F	232	84.0	30.2	45.4	49.7	361
496517	25 June 1966	R. S. Crossin	21°56′N, 159°46′W	F	237	87.6	34.8	44.2	48.4	347.2
496518	25 June 1966	R. S. Crossin	21°56′N, 159°46′W	M	240	84.5	34.1	46.0	50.6	425
496701	10 July 1966	L. N. Huber	06°19′N, 171°29′W	F	243	87.4	34.7	44.9	49.0	422

The Pacific Ocean Biological Survey Program of the Smithsonian Institution has collected 24 specimens since 1963, and Gerald Swedberg, Hawaii State Fish and Game Biologist on Kauai, obtained six more for the Smithsonian Institution (Table 3). Many of these specimens were killed in collisions with automobiles and a lighthouse tower. Of these 30 new specimens, 16 were from Kauai, three from three miles southwest of Kauai, eight from other pelagic central Pacific localities, one from Johnston Atoll, and two from Wake Island (Figure 1).

Table 3 presents the measurements of the 30 Smithsonian specimens plus those of nine others measured by the senior author. The measurements of Paris Musum Specimen 5099 (Table 1) are from Jouanin (1956).

Our measurements of the type and BPBM 1100 agree closely with those given by Loomis (1918) and Murphy (1952). Although Mathews and Hallstrom (1943) claimed to have measured the "type," their measurements correspond more closely with BPBM 1100 than with the actual type.

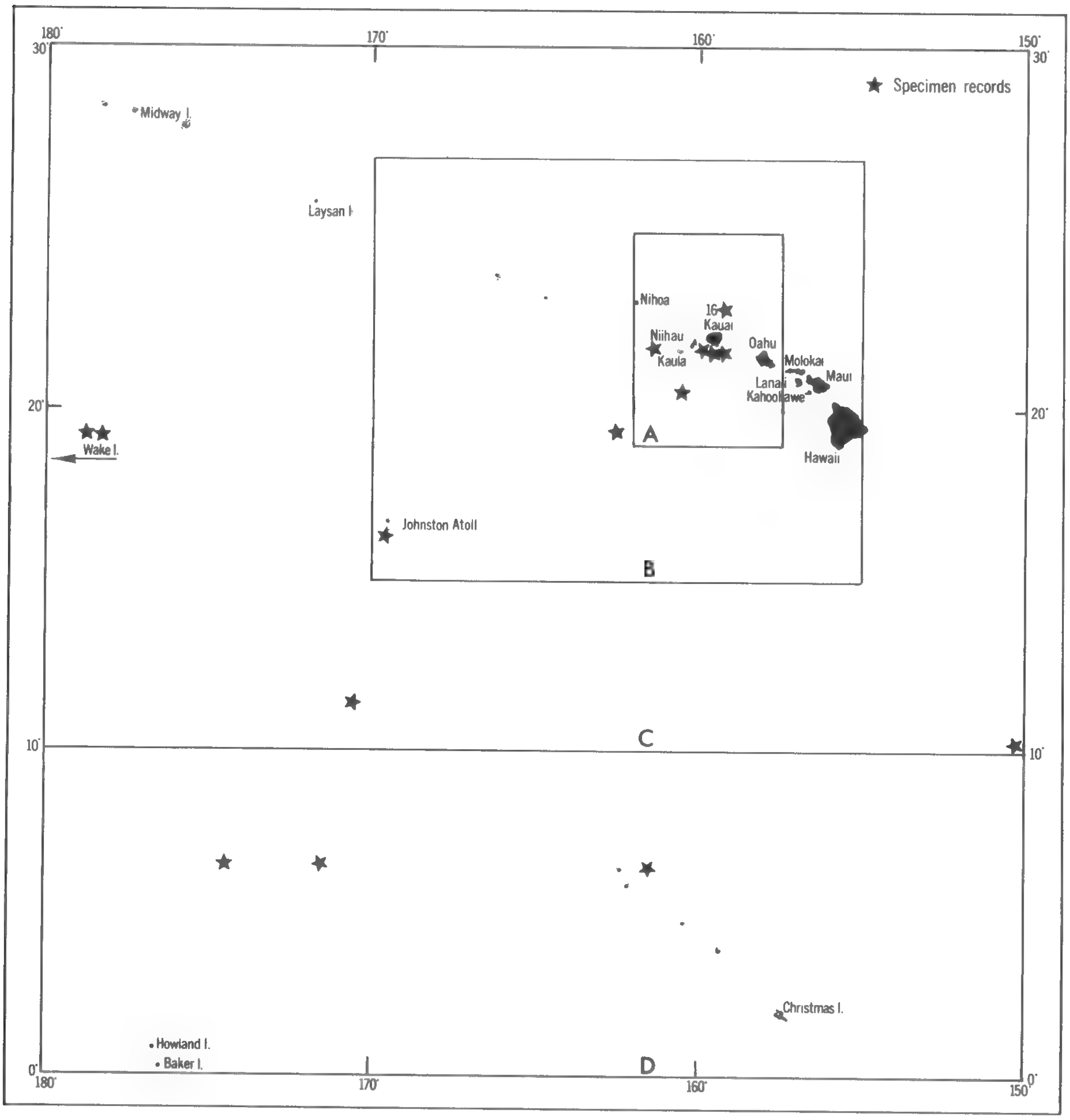
180°
170°
160°
150°
30°
20°
10°
0°
★ Specimen records
Midway I.
Laysan I.
Nihoa
16★
Kauai
Niihau
Kaula
Oahu
Molokai
Maui
Lanai
Kahoolawe
Hawaii
A
Wake I.
Johnston Atoll
B
C
D
Christmas I.
Howland I.
Baker I.

Figure 1. Map of the north-central Pacific Ocean showing the Hawaiian Islands and other localities where the Smithsonian Institution's specimens of Newell's Shearwater were collected. See the text for an explanation of Areas A, B, C and D.

Wing and tail measurements of the type are shorter than the means of the rest of our sample by more than two standard deviations. The outer primary on each side and all the rectrices are still in sheath. We conclude that the type was an immature bird since the normal adult molt pattern in Procellariidae is sequential, not simultaneous (J. M. Harrison *in* Thomson, 1964). If such is the case, either the date of collection as reported (spring 1894) is erroneous or the time of fledging of the specimen was anomalous with the hypothetical cycle we have pieced together from the occurrence of the birds on Kauai and at sea nearby. The natives in Pelekunu Valley, Molokai, told Bryan (1908) that "some birds were seen, or rather heard, throughout the year (?) [the parenthetical question mark is Bryan's], but that they became plentiful about the first of May," indicating an annual breeding cycle starting in the spring. Lockley (1942) and Harris (1966) showed that Manx Shearwaters are extremely regular in their breeding cycle, and that all lay their eggs within a month's time. If we assume that the Newell's Shearwater has breeding habits similar to the Manx Shearwater's (*P. p. puffinus*), it is more likely that the type was collected in the fall than in the spring.

We found no significant difference at the 95 per cent level in the means of the five standard measurements of males and females (see Table 4). Accordingly, the measurements of males, females, and those of birds whose sex was undetermined were lumped to increase the sample size for greater statistical significance in making comparisons with other populations. In two instances primary and rectrix molt caused unusually short measurements—i.e., further than two standard deviations from the mean. These were omitted from the samples. We have weight data for only 11 specimens, four males and seven females. Although there was large variability in the small samples, the mean weights of males and females from which the samples were taken were not statistically different at the 95 per cent level. The data in Table 4 indicate no sexual dimorphism in body weight or in lengths of wing, tail, culmen, and middle toe and claw.

The measurements of Murphy's (1952) two specimens (one molting all the rectrices) failed to show that tail measurements in *newelli* average 6 mm longer than in *opisthomelas* and 10 mm longer than in *puffinus* or *auricularis*. In other measurements our larger sample reflects no disagreement with Murphy's conclusions.

The stomach contents of five specimens contained an average of 105 squid lenses as well as partially digested remains of small fish and crustaceans.

Distribution in the Hawaiian Islands

Newell's Shearwater apparently breeds, or bred, only in the main Hawaiian Islands. No one has yet described its nest burrows, eggs, and downy young although before 1908 the Hawaiian natives knew the breeding habits of the bird well (Bryan, 1908). An old Hawaiian adage used in reference to parents who had only one child was: "The 'a'o [Newell's Shearwater] lays but a single egg" (Pukui and Elbert, 1957). By 1908 it had already been extirpated from most of the islands on which it occurred. We can be certain that it bred on Kauai, Molokai, and Maui; fairly certain that it bred on Hawaii; and believe that it probably bred on all the main Hawaiian Islands at one time. The evidence is as follows.

Hawaii

Although no specimen of a Newell's Shearwater has been collected on Hawaii, Munro (1960) wrote "It used to nest in the Waipio Valley, Hawaii,

TABLE 4

Dimensions and Weights of *Puffinus puffinus newelli*

Measurement	*Sample*	*Mean*	*Standard error*	*Confidence interval (.95) of population mean*	*Sample range*	*Standard deviation*	*Student's t-value for differences between means*
Wing	18F	236.5	1.47	233.4–239.6	227–249	6.25	−.3549
	10M	237.5	2.25	232.4–242.6	223–245	7.12	
	37F, M, & ?	237.4	1.02	235.4–239.4	223–249	6.19	
Tail	18F	85.0	.58	83.8–86.2	79.9–88.7	2.47	.3182
	10M	84.6	.98	82.4–86.8	79.3–88.8	3.11	
	36F, M, & ?	84.3	.46	83.3–85.3	78.9–88.8	2.75	
Culmen	18F	32.9	.33	32.2–33.6	30.2–34.8	1.41	−1.1131
	11M	33.4	.33	32.7–34.1	32.3–35.5	1.10	
	39F, M, & ?	33.2	.21	32.8–33.4	30.2–35.5	1.34	
Tarsus	18F	45.8	.29	45.2–46.4	44.4–48.3	1.22	.3629
	11M	45.6	.43	44.6–46.6	43.3–47.5	1.42	
	39F, M, & ?	45.8	.21	45.4–46.2	43.3–48.3	1.31	
Middle Toe and Claw	17F	48.7	.45	47.8–49.7	45.6–52.4	1.86	−1.2966
	11M	49.8	.64	48.4–51.2	47.3–54.3	2.13	
	37F, M, & ?	49.1	.36	48.4–49.8	45.6–54.3	2.18	
Weight	7F	382.2	11.92	353.0–411.4	342.5–422	31.54	−1.4245
	4M	407.0	10.11	374.8–439.2	389–425	20.22	
	11F, M, & ?	391.2	8.92	373.4–409.0	342.5–425	29.59	

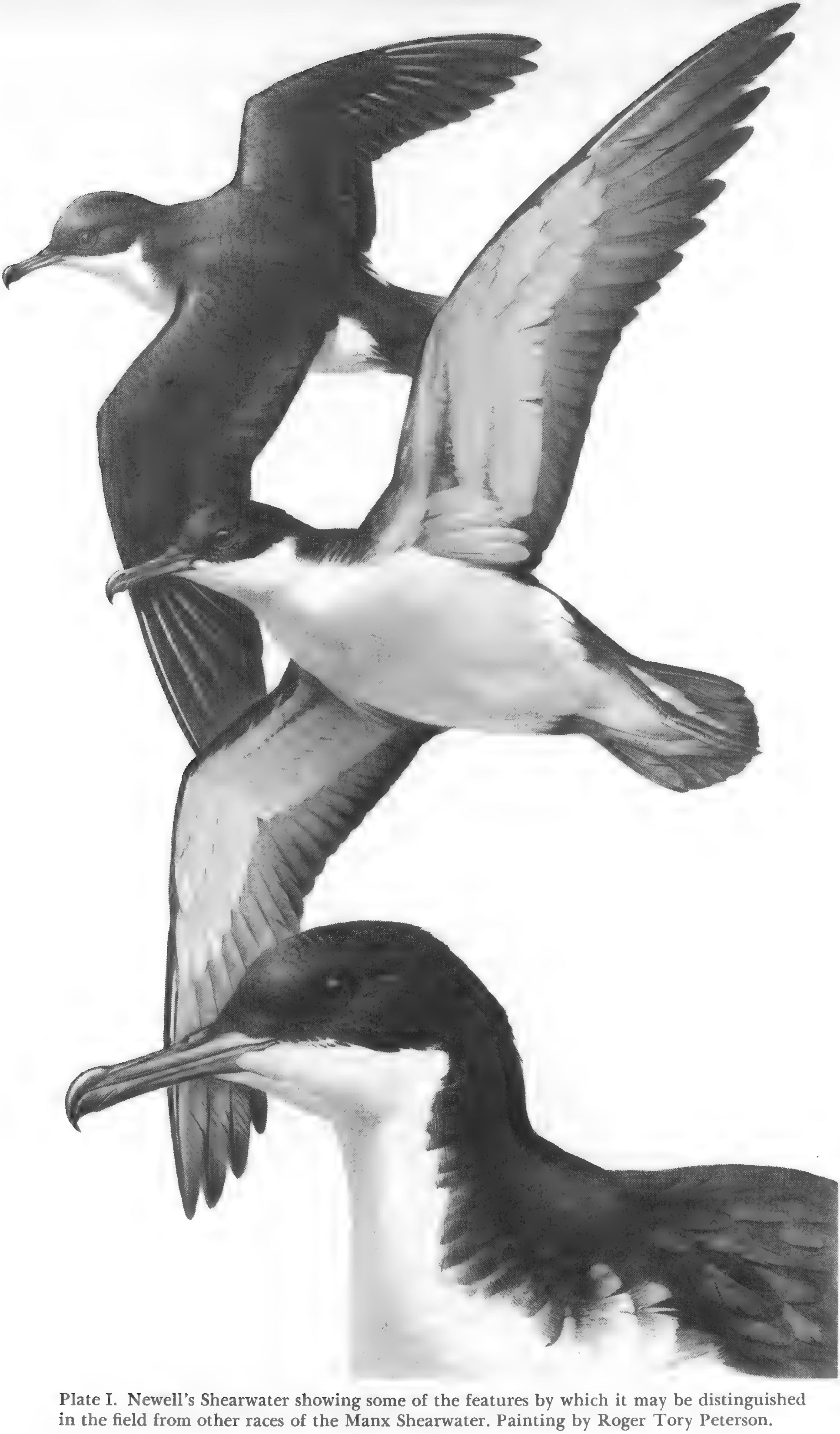

Plate I. Newell's Shearwater showing some of the features by which it may be distinguished in the field from other races of the Manx Shearwater. Painting by Roger Tory Peterson.

and the natives used it for food." He cited W. H. Meinecke who reported that stragglers came at intervals to a cliff, called Puuao, near Waiohinu, Hawaii, where their characteristic "a-o" calls were heard. Munro considered this good evidence that Newell's Shearwater bred in the locality because Pu-a-'a'o, the original place name, means a flock of 'a'os in Hawaiian.

Maui

Two specimens from Waihee Valley, the type locality, represent our knowledge of the Newell's Shearwater on Maui. It has not been reported there since 1894.

Molokai

Bryan (1908) presented evidence that Newell's Shearwater bred on Molokai when he described a trip to the steep slopes above Wailau Valley in June. The native Hawaiians he accompanied collected numerous Dark-rumped Petrels (*Pterodroma phaeopygia*) for food and remarked that, whereas they had taken several Newell's Shearwaters from burrows in the same area the previous year, they found none that year. The natives were aware of the distinguishing characters between the two birds.

Bryan also suggested that Mrs. Wilson's specimen was from a second breeding area, one on the slopes of the mountain separating Pelekunu Valley from Waikolu Valley and referred to on present-day maps as Puu Alii.

Newell's Shearwater has not been reported on Molokai since 1908.

Lanai

We have found no evidence to indicate that Newell's Shearwater ever bred on Lanai. Although Peters (1931) listed it as a breeding bird of Molokai and Lanai, we have been unable to determine the source of his information. Mathews and Hallstrom (1943) and Alexander (1954) probably based their accounts of the breeding range of Newell's Shearwaters on Peters' publication.

G. C. Munro, who lived on Lanai for many years and knew its birds better than any other ornithologist, failed to mention Lanai as a breeding locality for Newell's Shearwaters in his "Birds of Hawaii" (1960).

Oahu

Udvardy (1961) listed Oahu as a breeding locality for Newell's Shearwater. A specimen taken on 22 May 1964 at Aiea by F. Richardson, a specimen taken on 3 July 1961 from Honolulu by J. Bowles, and a healthy bird, reported by Hatch (1959), that was picked up at Honolulu Airport, then banded and released the following day are the only records we have found. We do not know whether these birds were stragglers from a breeding population in the Waianae or Koolau mountain ranges on Oahu or strays from another island.

Niihau

Although Udvardy (1961) speculated that Newell's Shearwater bred on Niihau, the only recent ornithological survey of Niihau, by Fisher (1951), did not mention it. Fisher reported birds he took to be Newell's Shearwaters at sea between Niihau and Kauai, but did not indicate from which island the birds were coming.

Kauai

Bryan and Seale (1901) wrote: "Mr. Gay states that it [Newell's Shearwater] is fairly common in certain cliffs in the mountains." Munro (1941) recorded Gay's comment to him in 1891 that it laid its eggs "in May and June in holes in the earth near the sea."

Table 5 summarizes the recent land records of Newell's Shearwater on Kauai. The appendix to this paper gives a chronological listing of these records with dates, locations, and sources of information.

TABLE 5

Summary of Recent Newell's Shearwater Records on Kauai

Location	*Number of birds recorded*
Hanalei	several
Hanalei Plantation Hotel	10
Kilauea Point	43
Kealia to Wailua	123
Lihue	14
Koloa-Lawai	12
Eleele-Hanapepe	2
Waimea Canyon	25
Na Pali Coast	9

The account by Pearsall (1947) of finding two Newell's Shearwaters in burrows with large downy chicks in September at Kilauea Point needs further corroboration. Fennell (1947) found no indication of Newell's Shearwaters breeding at Kilauea Point nor have Smithsonian Institution personnel in 10 visits since 1963. If Pearsall's account were accurate, it would have been not only the first evidence of Newell's Shearwater between 1908 and 1946, but also the only reference to its downy young. His description of the adult birds was accurate except that they have flesh-pink legs and feet not yellow, as he suggests. Early descriptions of Newell's Shearwater that indicated yellow legs and feet were made from dry specimens (Henshaw, 1902). Wedge-tailed Shearwaters (*Puffinus pacificus chlororhynchus*) nest abundantly at Kilauea Point and would have large downy young in September. Newell's Shearwaters are sometimes seen in close company with breeding Wedge-tailed Shearwaters at Kilauea Point and could conceivably have been mistaken for breeding birds.

The records presented in Figure 2 show several areas of concentration. These concentrations occur for two reasons: first, because of the attraction of Newell's Shearwaters to strong lights, and second, presumably because of proximity to their breeding grounds. On overcast nights from May to November, especially in the latter part of October when young birds fledge, Newell's Shearwaters may "rain" down at any well-lit location. Hutton's Shearwater (*Puffinus puffinus huttoni*) has shown a similar attraction to lights in New Zealand (Harrow, 1965). On the northern coast at Kilauea Point a big lighthouse casts its beam from a 200-foot-high promontory. As they circle the area, Newell's Shearwaters become blinded by the light and crash into the lighthouse or a smaller antenna tower. Six of 48 birds recorded by us at Kilauea Point and the nearby Hanalei Plantation Hotel were fatalities, and

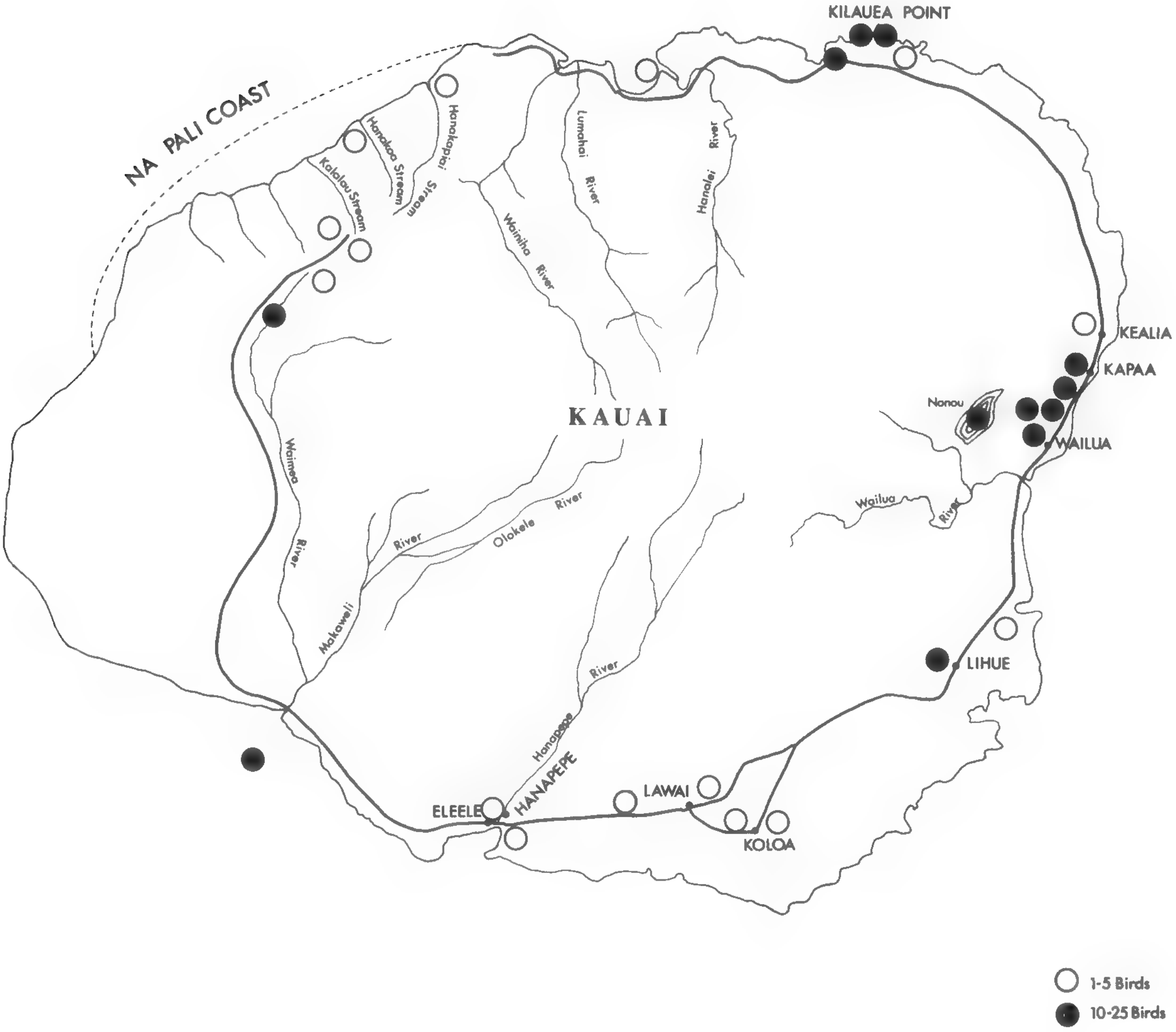
KILAUEA POINT
NA PALI COAST
Hanakapiai Stream
Hanakoa Stream
Kalalau Stream
Lumahai River
Hanalei River
Wainiha River
KAUAI
KEALIA
KAPAA
Nonou
WAILUA
Wailua River
Waimea River
Makaweli River
Olokele River
Hanapepe River
HANAPEPE
ELEELE
LAWAI
KOLOA
LIHUE
○ 1-5 Birds
● 10-25 Birds

Figure 2. Map of Kauai, Hawaiian Islands, showing where recent records of Newell's Shearwater were obtained.

the remaining 42, apparently healthy, were banded and released (see Figure 3). No Newell's Shearwaters were reported at the Hanalei Plantation Hotel after the bright, white ground lights were changed to subdued, colored ones in 1965.

The concentration at the Wailua River Bridge is probably due to a combination of street lights and proximity to what may prove to be a breeding locality on Nonou, or Sleeping Giant, Mountain. Only two of the 123 plus birds recorded along the coast road between Kealia and Wailua were found outside of the fledging period. The mortality rate here exceeded 50 per cent, probably because most birds came down on the highway and were struck by cars.

The concentration in the Waimea Canyon area is based on estimates of the numbers of birds calling in the canyon at night in April, May, and August (see Figure 4). Birds also call from the Kalalau, Hanakoa, and Waiahuakua Valleys along the Na Pali (northwestern) Coast and near Nonou Mountain on the east coast. Calling plays an important role in courtship or nest location with the North Atlantic population of the Manx Shearwater

(Lockley, 1942), and probably with Newell's Shearwaters as well. It may therefore prove a reliable indicator of breeding localities. The flight-call of the Newell's Shearwater is a series of two to five penetrating, harsh, rasping inhale and exhale notes, which can be heard at a considerable distance. Since the calls of shearwaters are difficult to characterize, any comparison between the calls of Newell's and the North Atlantic Manx Shearwaters, on the basis of written descriptions, is of questionable value. Lockley (1942) and W. R. P. Bourne (*in* Palmer, 1962) describe the flight-call of the North Atlantic Manx Shearwater as a sort of crowing, which would fit Newell's Shearwater's flight-call as well.

We have heard birds calling in all the valleys we have checked at night during the breeding season, and we suspect that Newell's Shearwaters probably nest in moderate numbers in most of the valleys of Kauai.

Population Size and Predation

From recent observations we conclude that Kauai is now the primary and possibly unique breeding locality of Newell's Shearwater. We believe its population to be at least in the low thousands and base our estimate on the numbers recorded at various locations around Kauai in addition to the numbers encountered at sea, especially within 100 miles of Kauai (see following section). Both on Kauai and at sea the numbers actually observed were only a fraction of the total population, since the sampling was never constant or comprehensive.

The mongoose (*Herpestes auropunctatus*) is an efficient predator of many ground-dwelling birds and mammals. It is probably more than coincidence that, of the islands on which Newell's Shearwater is known to have bred, this bird has been extirpated on those to which the mongoose was introduced and survives on Kauai where the mongoose was not introduced. It may breed on Lanai and Niihau, both mongoose-free as well, but evidence to confirm or deny this is lacking.

On Kauai, feral cats which are abundant over most of the island undoubtedly represent the greatest predation threat to Newell's Shearwaters. Feral dogs, also present in smaller numbers, probably account for some predation. In addition, rats (*Rattus rattus, R. norvegicus,* and *R. exulans*) are present. *R. rattus* probably plays the most important role of the three in predation (P. Quentin Tomich, *in litt.*)

Predation pressures no doubt restrict Newell's Shearwater in its breeding habitat to valley walls whose precipitous sides are relatively inaccessible. Many such areas exist on Kauai. Certainly the bird's docile nature would make it easy prey for mammalian predators. Control programs to reduce the feral populations of cats and dogs, as well as the continued exclusion of the mongoose from Kauai, should provide sufficient protection to insure the bird's future existence.

There are several islets offshore from some of the main Hawaiian islands. Although most are predator-free and support seabird colonies—e.g., Moku Manu and Manana Islands offshore from Oahu (Richardson and Fisher, 1950)—Newell's Shearwater has not colonized them. Some populations of *Puffinus puffinus* are evidently restricted to higher elevations (Harrow, 1965), whereas others nest on islets near sea level (Krueper, 1863). Although it would appear to be to the advantage of Newell's Shearwater to colonize offshore islets rather than to be extirpated by the mongoose on the main islands, some unknown mechanism evidently prevents it from making any such move.

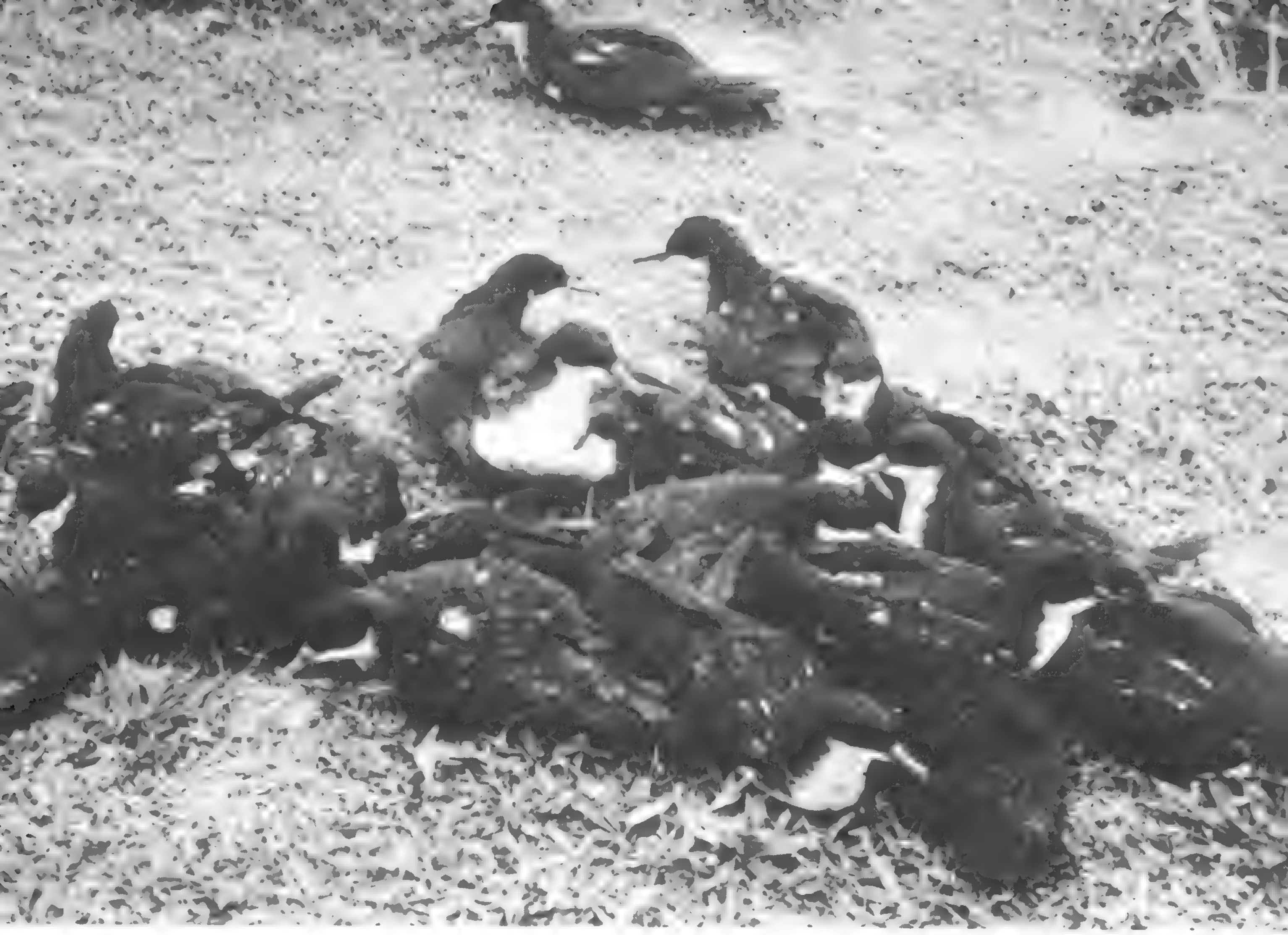

Figure 3 (*above*). A group of 25 Newell's Shearwaters which gathered at Kilauea Point, Kauai, on 4 May 1965 near the base of the lighthouse on an overcast, windless night. Most of the birds flew away unaided the following morning; a few needed to be "launched" into the air.

Figure 4 (*below*). Waimea Canyon, Kauai, where Newell's Shearwaters have been heard calling at night. The birds probably nest in burrows in the talus slopes on the canyon walls.

Distribution at Sea

In 1,444 days of observation in the Pacific Ocean by Smithsonian Institution personnel between 1963 and 1966, 1,742 Newell's Shearwaters were recorded. Nearly all of these sightings were made in the north-central Pacific (Latitudes 148° W to 180°, Longitudes 0° to 30° N). They have been recorded outside of this area just five times, twice on Wake Island, once on Saipan in the Marianas (Jouanin, 1956), once 40 miles south of the Equator near Baker Island, and once 41 miles north of 30° N north of the Leeward Hawaiian Islands.

Table 6 shows that from December through February Newell's Shearwater is almost entirely absent from the north-central Pacific. That it has not been recorded elsewhere during these months reflects the scantiness of at-sea observation data gathered across most of the Pacific.

TABLE 6

Numbers of Newell's Shearwaters Observed in North-central Pacific Ocean by Month

Month	*Total birds*	*Birds/day of observation*
January	3	.05
February	7	.07
March	27	.21
April	49	.37
May	477	4.77
June	164	1.38
July	207	1.90
August	559	4.54
September	149	1.31
October	71	.38
November	24	.15
December	5	.04
Total	1,742	1.21

Whether Newell's Shearwaters perform a clearcut migration to a specific area of the Pacific during the (northern) winter or simply disperse in several directions is not yet clear. The two records from Wake Island and one from Saipan in the Marianas were during the breeding season and thus lend little evidence to support either dispersion theory.

Figure 5 provides ample evidence that heavy concentrations of Newell's Shearwater feed at sea near Kauai and Niihau. Only flocks actually feeding are shown.

The largest number of Newell's Shearwaters recorded at one time was about 150. They were part of an immense mixed feeding flock of about 4,200 birds on 20 May 1966. The other sightings of large numbers indicated in

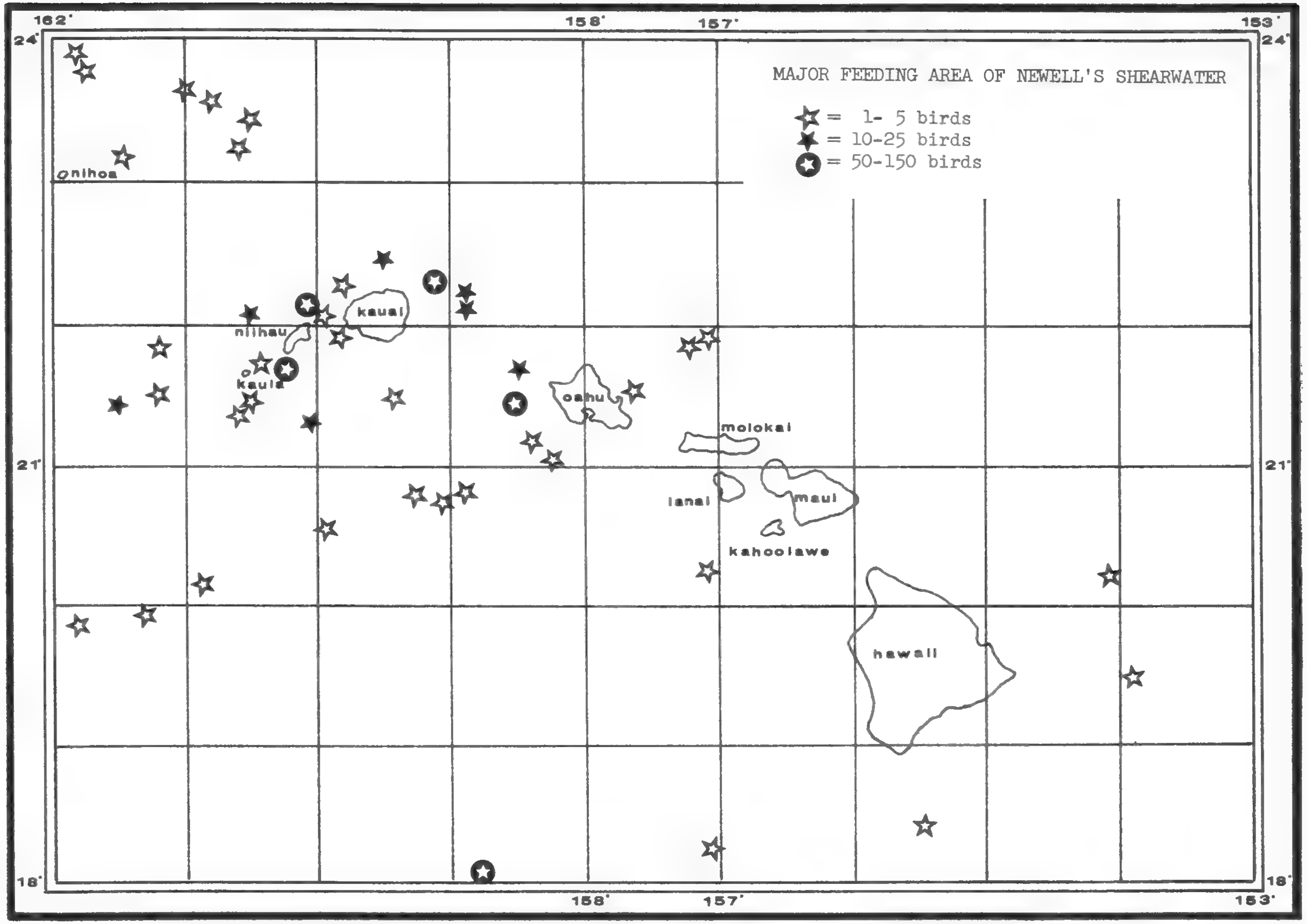
MAJOR FEEDING AREA OF NEWELL'S SHEARWATER
☆ = 1- 5 birds
★ = 10-25 birds
✪ = 50-150 birds
162°
158°
157°
153°
24°
21°
18°
nihoa
niihau
kaula
kauai
oahu
molokai
lanai
maui
kahoolawe
hawaii

Figure 5. Map of the main Hawaiian Islands showing the major feeding area of Newell's Shearwater.

Figure 5 consisted of 90±, 60+, 56, and 50 birds each. On 16 August 1966, the day on which the sighting of 50 birds was made, 289 Newell's Shearwaters were recorded.

For purposes of discussion we have divided the north-central Pacific into Areas A, B, C, and D in order of increasing distance from Kauai (see Figure 1). Highest density figures were recorded in Area A and second highest in Area B. Area D consistently maintained higher densities than Area C, although the latter was closer to the breeding grounds. Area D supports a high density of other seabird species as well. Local areas of enrichment occur in the water in Area D, due to constant turnover of nutrients along the boundaries of the North Equatorial Current, Equatorial Countercurrent, and South Equatorial Current, as well as comparative shallowness (often less than 30 meters depth) of the underlying subarctic water type which is richer in nutrients than the overlying equatorial water (Sverdrup *et al.,* 1942). High local enrichment results in an increase of plankton productivity, which in turn affects seabird distribution, even though seabirds are several links removed on the food chain. Increased food availability in Area D may be sufficient stimulus to cause birds to fly a greater distance to a more certain food source.

However, Harris (1966) suggested that since many Manx Shearwaters in the North Atlantic feed their chicks at least two nights out of three, and since the primary feeding grounds of the breeding birds of Skokholm and other colonies of the Irish Sea are within 200 miles of the breeding grounds, most of the birds found in the Bay of Biscay north of Spain where Manx Shearwaters occur in large numbers during the breeding season are subadult and nonbreeding adults. Area A is undoubtedly the primary feeding area of breeding Newell's Shearwaters during the breeding season, and Area D may serve as the feeding ground for subadults and nonbreeding adults, as does the Bay of Biscay for North Atlantic Manx Shearwaters.

Two of the four birds collected in Area D during the breeding season were undergoing primary and rectrix molt. We suspect these were subadult

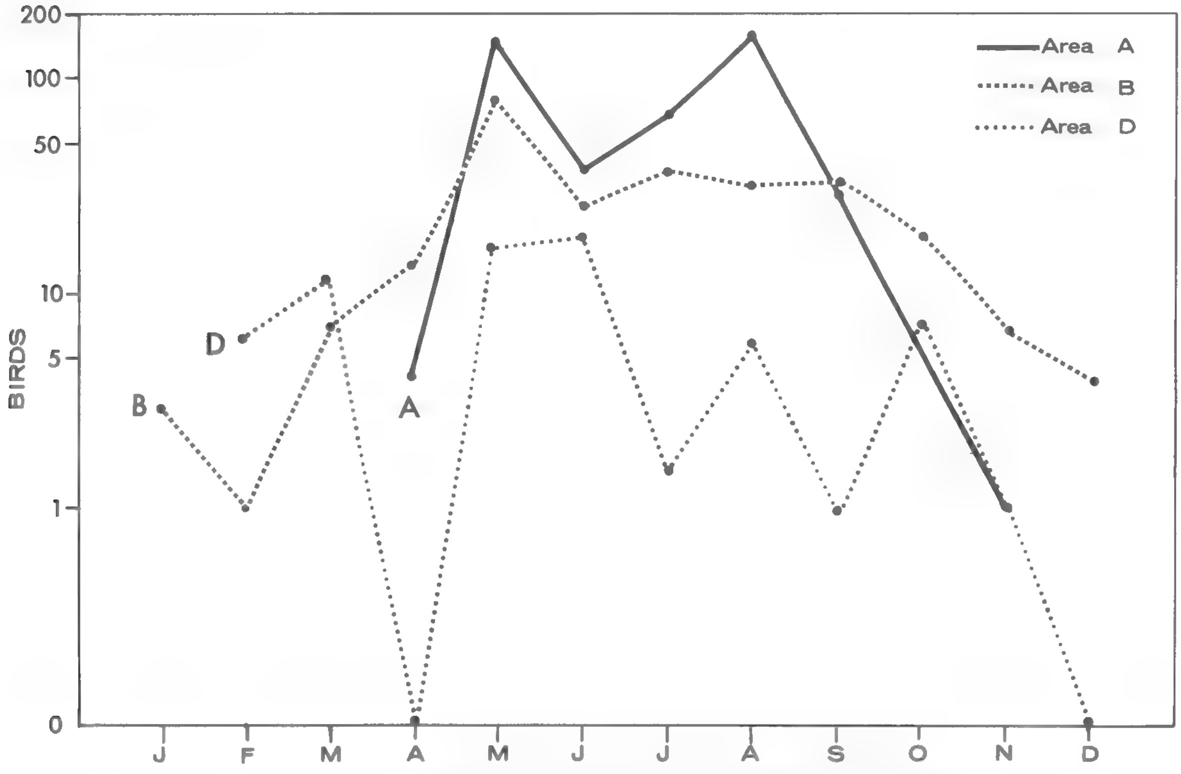

Figure 6. Cycles of seasonal abundance of Newell's Shearwater in different parts of the north-central Pacific Ocean.

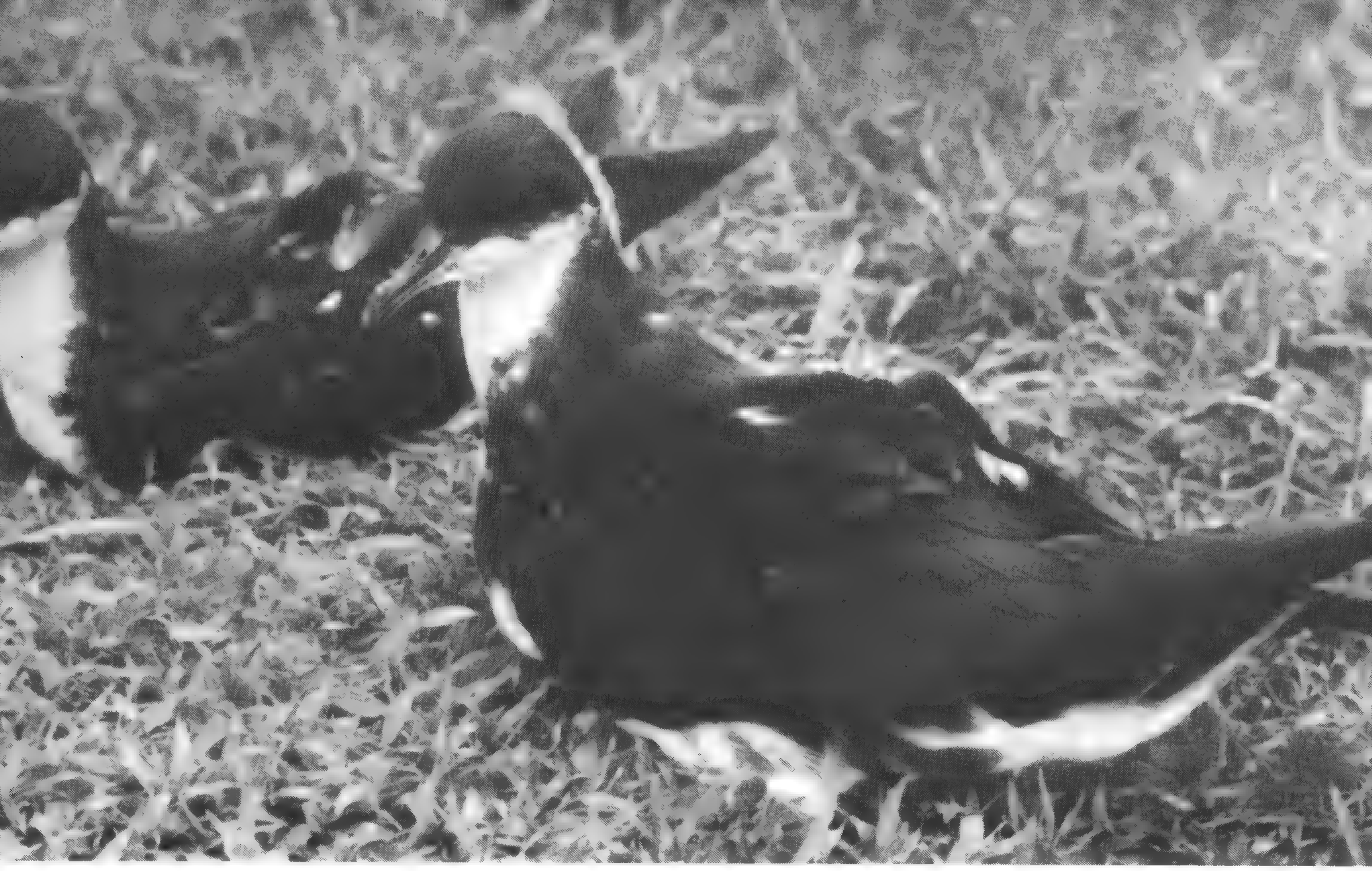

Figure 7. Two Newell's Shearwaters at Kilauea Point, Kauai, on 29 October 1964. Note the pale gray down clinging to the nape of the nearer bird.

birds whose molt cycle was not yet synchronized with that of breeding birds which is completed by the beginning of the breeding season. Only one of the 25 birds taken on and around Kauai between May and November was undergoing primary and rectrix molt. It was collected on 4 May 1965 at the start of the breeding season. The only bird collected between December and April was a molting bird in Area D on 3 February 1966.

Area D was the first area to show an increase in the numbers of Newell's Shearwaters in the spring. The numbers in Areas A and B both reached peaks in May, but the peak in Area A was sharper—i.e., more rapid in developing and involving higher numbers. A second peak in August may be explained by the presence of young nonbreeders and breeding birds which are no longer brooding chicks in the breeding area. Thereafter the numbers decline gradually until December when most birds have left the north-central Pacific.

A graphic presentation of seasonal population build-up and decline in Figure 6 shows that the area closest to the breeding area (Area A) has greater densities than Area B only from May to August. Area D shows a build-up and a second peak two months prior to the peaks in Area A in each case. Certainly some, perhaps most, Newell's Shearwaters pass through Area D on the way to their breeding grounds.

Breeding Cycle

We can support a case for the probable breeding phenology of Newell's Shearwater, as suggested by Richardson (1957), on the basis of indirect evidence alone. Birds first arrive in the breeding area early in April. We heard only an occasional call at night in Waimea Canyon, Kauai, at this time in 1965. The greatest numbers of birds were heard calling at night in May 1965. This corresponds to a density peak at sea around Kauai at the same time. Natives on Molokai told Bryan (1908) that they heard large numbers calling after the first of May. Egg-laying probably takes place at the beginning of June.

Incubation in June and July probably accounts for the slight decrease in numbers of birds observed at sea around Kauai in these months. Lockley (1942) showed that with Manx Shearwaters in the North Atlantic at least one parent is present at the nest burrow throughout incubation. If this is true of Newell's Shearwaters as well, we should expect the numbers observed at sea at this time to decrease.

The second peak in numbers, observed at sea near Kauai in August, probably corresponds to the period of intermittent nest attentiveness, beginning one or two weeks after the eggs hatch, during which adults return to burrows only to feed their chicks (Lockley, 1942). Returning subadults may also help to swell the August totals at sea.

Flying birds of the year with patches of down have been recorded several times in October (Figure 7). Of our 10 October specimens from Kauai, eight had new plumage and two had worn plumage. All had small gonads. The latter two were probably adults, and the former eight immatures. Possibly most of the birds still in the vicinity of Kauai in October are immatures, and most adults have left the area.

By November most birds have left the breeding grounds. Fewer Kauai records exist for November than for October. Numbers decrease at sea near Kauai as well.

The breeding cycle of Newell's Shearwater is apparently quite similar to, but one month behind, that of the North Atlantic Manx Shearwater described by Lockley (1942). One small difference lies in the shorter length of time which Newell's Shearwaters evidently spend in the breeding area prior to egg-laying. According to our hypothetical schedule, Newell's Shearwaters only spend one, possibly two, months, whereas Manx Shearwaters in the North Atlantic spend two to three months on the breeding grounds prior to egg-laying.

We can offer three possible explanations. First, Newell's Shearwater may be subject to greater predation pressure, which would place a premium on curtailed courtship activities on the ground in or near the nest burrows. Second, it may undertake a lengthier migration than the North Atlantic Manx Shearwater, which would prevent birds from returning so soon to the breeding area. Third, there may be no period of absence within the initial courtship and egg-laying as there is with the North Atlantic Manx Shearwater (Harris, 1966).

We can construct a hypothetical life cycle from this evidence. The breeding cycle begins in April with the appearance of breeding birds in fresh plumage on Kauai. Courtship takes place until the beginning of June when most eggs are probably laid. Eggs hatch toward the end of July and the chicks are large enough to be left unattended, except for frequent feeding, in August. Subadults and nonbreeding adults which have spent the preceding three months, many undergoing molt, in a secondary feeding area south of the Hawaiian Islands between the Equator and 10° N Latitude now join the breeding adults on the primary feeding grounds around Kauai and Niihau. Most adults leave the breeding area for unknown winter feeding grounds by the beginning of October. Chicks fledge in October and early November and leave immediately for the winter feeding area. There are almost no Newell's Shearwaters in the north-central Pacific by the middle of November. Adults probably molt during this contra-nuptial season. Almost all birds remain in the winter feeding area until March when some, probably breeding birds, enter the secondary feeding area north of the Equator. The breeding birds appear once again on Kauai in April and the cycle has come full turn.

Summary

Newell's Shearwater is the north-central Pacific Ocean race or representative of the circumglobal superspecies *Puffinus puffinus*. Only seven specimens were known prior to 1954. Four of these appear to be lost. This race was considered extinct in the first half of this century. Many recent records show that it survives in the thousands at least on Kauai in the Hawaiian Islands. There it is free from predation by the mongoose, which probably caused its extirpation from Maui, Molokai, and Hawaii, but not by the feral cats and dogs and rats which inhabit Kauai in uncontrolled abundance.

Thirty-nine of the 46 specimens known to have been collected were examined. Thirty are recent specimens now at the Smithsonian Institution. Measurements of 11 males and 18 females indicated no sexual dimorphism. Newell's Shearwater differs appreciably from all other populations of *Puffinus puffinus* only in its longer tail.

Newell's Shearwater is common at sea in the north-central Pacific from March to November, becoming abundant within 100 miles of Kauai and Niihau from May to September. It first appears on Kauai in April. Its egg is presumably laid at the beginning of June and young fledge in October. From December through February it is almost entirely absent from the north-central Pacific, suggesting an extensive dispersion or migration to unknown feeding grounds during the contra-nuptial season.

Acknowledgments

We would like to extend our thanks to past and present members of the Pacific Ocean Biological Survey Program for their long hours of field and clerical work in gathering and recording these data. We owe a debt of gratitude to the U. S. Department of Interior, whose Bureaus of Sport Fisheries and Wildlife and Commercial Fisheries lent us support countless times. We are also deeply obliged to the State of Hawaii, Division of Fish and Game, and especially to Gerald Swedberg, Fish and Game Biologist on Kauai, for permission to use his field notes on Newell's Shearwater from 1962 to 1965. Mrs. Anne Keenan Poulson patiently prepared the figures. Roger Tory Peterson graciously consented to do the plate. George E. Watson gave the manuscript a critical reading.

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(Continued on page 185)

APPENDIX

Recent Newell's Shearwater Records from Kauai, Hawaiian Islands

Date	*Number*	*Status*	*Location*	*Source*
September 1946	4	Breeding: 2 adults with downy young	Kilauea Point	G. Pearsall, 1947
4–6 July 1946	0	No evidence found of breeding activity or occurrence	Kilauea Point	C. Fennell, 1947
October 1956	1	dying	Kapaa Beach	Anonymous, 1956
8 October 1956	1	specimen	Koloa	S. D. Ripley, 1957
5 November 1956	1	specimen	Kilauea Point	Peabody Museum, collected by J. Bowles
October ? 1957	1	specimen	Kapaa (?) Beach	T. H. Hadley, 1961
31 July 1960	1	specimen	Wailua	Bishop Museum
Late October 1961	48	dead along road	Kealia to Wailua	T. H. Hadley, 1961
September 1962	47	downed	Wailua	G. E. Swedberg, pers. commun.
October 1962	2	downed, banded, and released		G. E. Swedberg, pers. commun.
	1	fell out of sky exhausted	Lihue	G. E. Swedberg, pers. commun.
	6	dead along highway		G. E. Swedberg, pers. commun.
4–8 September 1963	?	evening flights	Hanalei	W. M. Ord, 1963
November 1963	1	exhausted		G. E. Swedberg, pers. commun.

APPENDIX (continued)

Date	*Number*	*Status*	*Location*	*Source*
Summer 1964	?	heard	Na Pali Coast	Richardson and Bowles (1964)
	4	dead	East Coastal Highway	Richardson and Bowles (1964)
	1	dead	Kapaa Beach	Richardson and Bowles (1964)
	1–6	flying inland in evenings	Kapaa	Richardson and Bowles (1964)
6 July 1964	1	specimen	Hanalei Plantation Hotel	W. B. King, field notes
5–6 August 1964	ca 25	heard	Waimea Canyon	W. B. King, field notes
	ca 5	heard	Kalalau Valley	W. B. King, field notes
Fall 1964	2	live	Kokee Radar Tracking Station	W. B. King, field notes
21 September 1964	1	picked up alive, died later, specimen	Kalaheo	G. E. Swedberg, pers. commun.
11 October 1964	2	dead, specimens	Wailua	G. E. Swedberg, pers. commun.
12 October 1964	2	dead, specimens	Lihue	G. E. Swedberg, pers. commun.
13 October 1964	1	live	Wailua	G. E. Swedberg, pers. commun.
	1	dead, specimen	Wailua	G. E. Swedberg, pers. commun.
19 October 1964	1	live	Lihue	G. E. Swedberg, pers. commun.
25 October 1964	1	dead, specimen	Lihue	W. B. King, field notes
25 October 1964	1	dead, specimen	Hanapepe	W. B. King, field notes
29 October 1964	2	dead, specimens	Kilauea Point	W. B. King, field notes
29 October 1964	16	banded and released	Hanalei Plantation Hotel and Kilauea Point	W. B. King, field notes
30 October 1964	1	live with broken neck, specimen	Wailua	W. B. King, field notes
November 1964	1	dead	—	G. E. Swedberg, pers. commun.
14 November 1964	1	live	Lawai	G. E. Swedberg, pers. commun.
April 1965	1	?	Kilauea	G. E. Swedberg, pers. commun.
	1	?	Lawai	G. E. Swedberg, pers. commun.
6 April 1965	1	heard	Hanakoa Valley, Na Pali Coast	W. B. King, field notes
7 April 1965	1	heard	Waimea Canyon Lookout	W. B. King, field notes

APPENDIX (continued)

Date	*Number*	*Status*	*Location*	*Source*
23 April 1965	1	live	Lawai	W. B. King, field notes
1 May 1965	ca 25	heard	Waimea Canyon Lookout	W. B. King, field notes
4 May 1965	3	dead, specimens	Kilauea Point	W. B. King, field notes
	25	banded and released	Hanalei Plantation Hotel and Kilauea Point	W. B. King, field notes
	1	dead, specimen	Lihue (?)	W. B. King, field notes
	10	heading out to sea at 6:00 am	One mile offshore of Waimea Canyon	W. B. King, field notes
July 1965	several	—	Lawai and Wailua	G. E. Swedberg, pers. commun.
	1	dead	Lawai-Koloa Road	G. E. Swedberg, pers. commun.
	1	dead	Wailua	G. E. Swedberg, pers. commun.
6–8 August 1965	2	heard	Waiahuakua Valley	W. R. Donaghho, 1965
7 October 1965	1	dead	Wailua	G. E. Swedberg, pers. commun.
16 October 1965	1	live, released	Lihue	G. E. Swedberg, pers. commun.
18 October 1965	1	dead	Hanamaulu	G. E. Swedberg, pers. commun.
21–23 October 1965	11	dead	Wailua	G. E. Swedberg, pers. commun.
4 November 1965	1	dead	Nonou Mountain	G. E. Swedberg, pers. commun.
	2	dead	Lihue	G. E. Swedberg, pers. commun.
	1	live	Lihue	G. E. Swedberg, pers. commun.
5 November 1965	2	dead	Lawai-Koloa Road	G. E. Swedberg, pers. commun.
	2	live	Lihue	G. E. Swedberg, pers. commun.
8 November 1965	1	live	Eleele	G. E. Swedberg, pers. commun.
22 November 1965	2	dead	Lawai-Koloa area	G. E. Swedberg, pers. commun.
2 November 1966	3	banded and released	Kilauea Point	T. J. Lewis, pers. commun.
	1	dead	Lihue	T. J. Lewis, pers. commun.
January 1967	1	previously unreported specimen at Kokee Museum	Kokee	D. I. Hoff, pers. commun.

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PACIFIC OCEAN BIOLOGICAL SURVEY PROGRAM,
SMITHSONIAN INSTITUTION, WASHINGTON, DISTRICT OF COLUMBIA

ECOLOGICAL ADAPTATIONS IN THE LIFE HISTORY OF THE BROWN BOOBY AT ASCENSION ISLAND

K. E. L. SIMMONS

Drawings by Robert Gillmor

The Brown Booby (*Sula leucogaster*), the Masked Booby (*S. dactylatra*), and the Red-footed Booby (*S. sula*) are pantropical seabirds of "the blue waters"—the impoverished seas with a low density of surface plankton and, hence, of surface-living prey-fish. All three occur at remote Ascension Island (Figure 1) in the mid-central Atlantic Ocean, 7°, 57′ South Latitude and 14°, 22′ West Longitude.

Large numbers of boobies and other seabirds once bred on the lowland plains of 38-square-mile Ascension, but with human settlement in the early nineteenth century and the subsequent introduction of domestic cats, their populations were soon decimated. Today all the boobies and most of the other seabirds nest beyond reach of feral cats on Boatswainbird Island off the coast and on small inshore stacks; but, while the Brown Booby and Masked Booby still breed in fair numbers, the Red-footed Booby is nearly extirpated.

The Centenary Expedition of the British Ornithologists' Union studied the biology of the seabirds at Ascension for some 18 months in 1957-1959. Stonehouse (1960) gives a general account of the work and, in the special Centenary Expeditions volume of *The Ibis,* Dorward (1962a and 1962b) has two papers on boobies, both of which provided a basis for my own studies.

During my two years residence on Ascension in 1962-1964 and a three-week visit in 1966, I watched Brown Boobies almost daily on and around their colonies on the first two of a series of five inshore stacks off the northwest coast above Georgetown, the principal settlement (Figure 2). Brown Noddies (*Anous stolidus*) also nested on these stacks. The present paper, based on a comprehensive monograph to be published elsewhere, is an account of some aspects of my studies of Brown Boobies against a background of adaptive themes.

General Aspects

At Ascension both the adult male and female Brown Boobies are predominantly brown with a white belly (Figure 3). The straight line of demarcation across the breast is a highly characteristic feature, the only other white being in the center of the underwing (Figure 4). The brown on the head, neck, upper breast, and upper back is darker than the rest of the

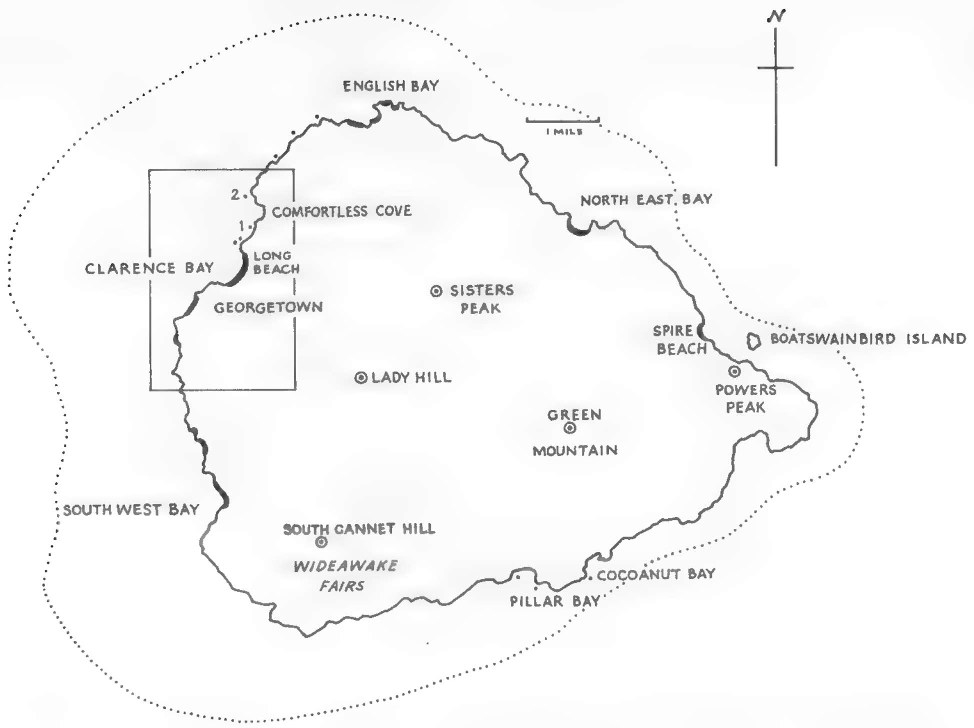
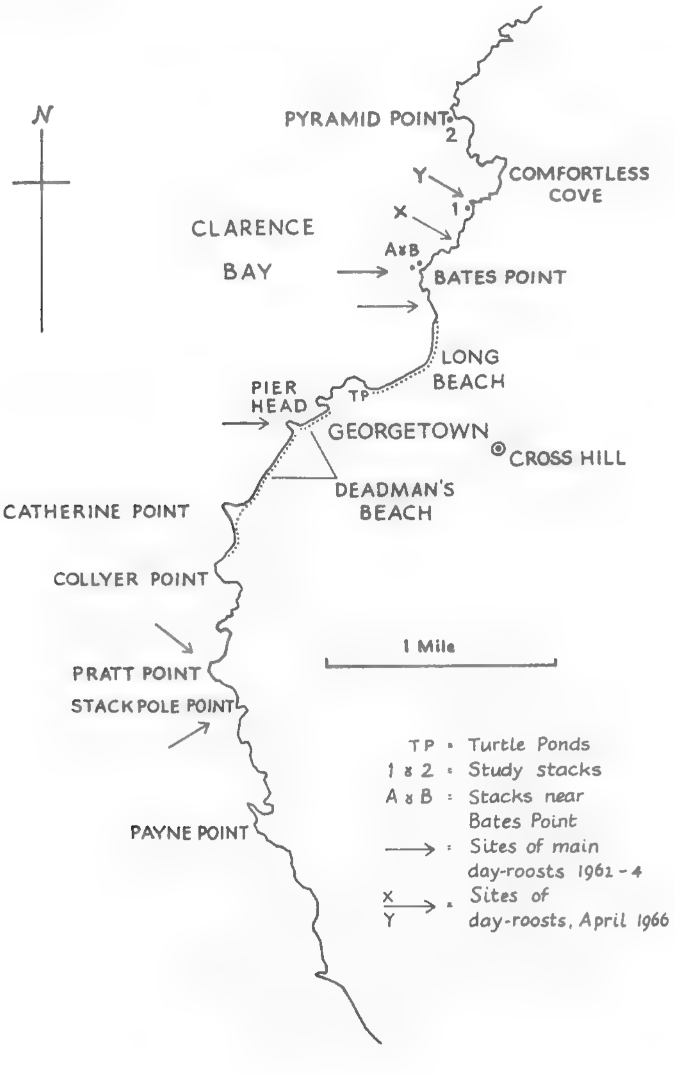

N
ENGLISH BAY
1 MILE
NORTH EAST BAY
2.
1.
COMFORTLESS COVE
CLARENCE BAY
LONG BEACH
GEORGETOWN
SISTERS PEAK
SPIRE BEACH
BOATSWAINBIRD ISLAND
POWERS PEAK
LADY HILL
GREEN MOUNTAIN
SOUTH WEST BAY
SOUTH GANNET HILL
WIDEAWAKE FAIRS
COCOANUT BAY
PILLAR BAY

Figure 1 (*above*). Map of Ascension Island in the mid-central Atlantic Ocean. The larger beaches are shown by thick lines, the 100-fathom contour by dotted line. The rectangle encloses the main study area (see Figure 2).

Figure 2 (*below*). Map of the main study area on the northwest coast of Ascension Island. In 1962 the Brown Boobies did much inshore fishing in this area, many birds resting in "day roosts" on rocks along the coast after congregating to feed. In April 1966 the boobies also used certain rocks as "hunting clubs" from which to launch out after prey that were borne inshore by the heavy swell.


N
PYRAMID POINT
2
Y
COMFORTLESS COVE
X
1
CLARENCE BAY
A & B
BATES POINT
LONG BEACH
PIER HEAD
TP
GEORGETOWN
CROSS HILL
DEADMAN'S BEACH
CATHERINE POINT
COLLYER POINT
1 Mile
PRATT POINT
STACKPOLE POINT
PAYNE POINT
TP = Turtle Ponds
1 & 2 = Study stacks
A & B = Stacks near Bates Point
→ = Sites of main day-roosts 1962-4
X Y → = Sites of day-roosts, April 1966

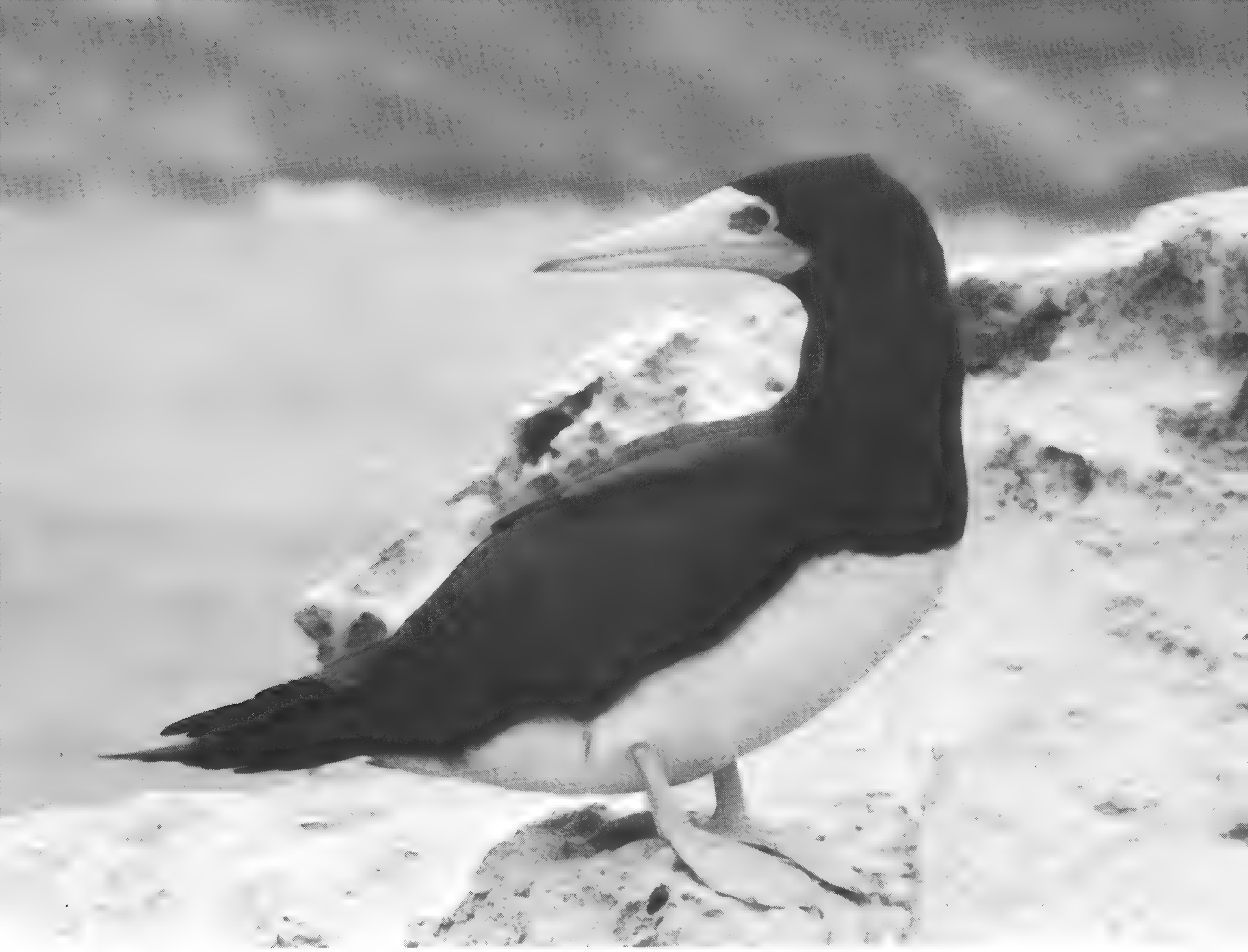


Figure 3. Female Brown Booby Looking-out to sea from the site-perch in her nesting territory. Note the species-specific plumage, including the dark brown "cowl." Photograph by D. F. Dorward, British Ornithologists' Union Centenary Expedition, 1957-1959, Boatswainbird Island off the east coast of Ascension Island.

plumage and forms a "hood" or a "cowl." This dark plumage is unusual in the genus *Sula;* all of the other five species (except for the dark phases of polymorphic *S. sula*) are predominantly or largely white with a white frontal aspect.

Sexual Dimorphism

Though identical in plumage, the sexes differ in size and in the color of their fleshy parts. Females are noticeably larger and heavier than males, with stouter and coarser bills. The facial skin, including the thick eye-lids, is pale yellow except for a blackish "false-eye" patch immediately in front of the eye. The feet are also pale yellow, showing little if any seasonal or cyclical variation.

Adult males are distinct from females at all times in soft-part colors which vary according to the breeding stage. The male in "non-breeding" color resembles the female but usually has a greenish bloom to his upper facial skin, a bluish eye-skin, and greenish feet. In full "display" or "courtship" color, in the pre-egg stage of the reproductive cycle, his facial skin, gular area, and feet become deep chrome-yellow and his eye-skin bright blue. The yellow fades during incubation and by the time he is attending the chick he is in "parental" or "post-courtship" color, with his facial skin a whitish or bluish wash and his feet green. A knowledge of these color changes proved useful to me in assessing the reproductive activity in the colonies in 1966.

The voices of the sexes are very different; females give loud, honking calls; males much quieter, whistling calls. The range of social behaviors, while similar in both, differs mainly in intensity and frequency due to different states of motivation. Only the male has the advertising Saluting display (see below).

Plumages of Young

There are noticeable differences among the various age groups of Brown Boobies. The chicks are covered with white down; juveniles develop a brown plumage in which there is no white, though a faint line of demarcation on the breast and a somewhat paler brown belly foreshadows the adult pattern (Figure 5). In young birds the color of the bill, eye, and face is uniformly gray. As the juvenile gets older, its facial skin gradually lightens to a yellowish tone like the female's, its feet change from flesh-orange to pale yellow, and the bill becomes paler. The near-adult resembles the adult female in appearance and voice but one can identify the young male by his smaller size and dark, grayish eye-skin.

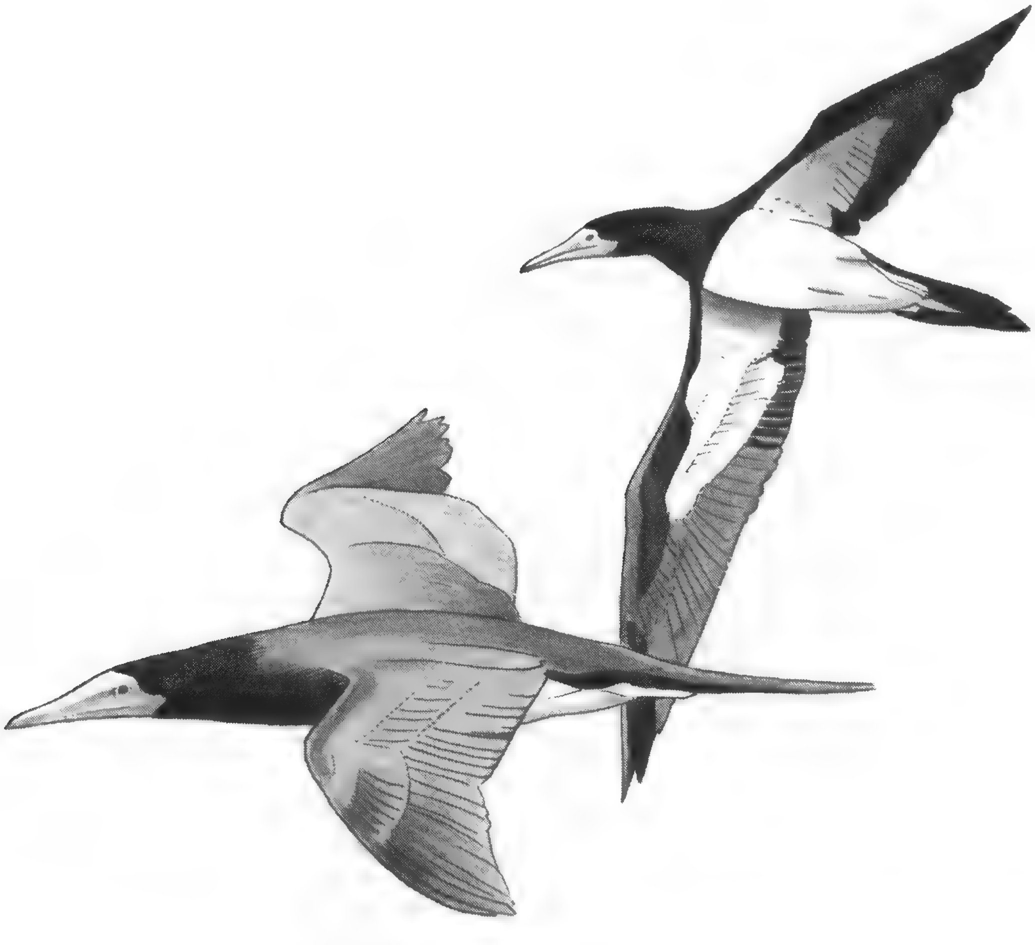


Figure 4. Female Brown Boobies in flight, showing the species-specific demarcation of the plumage from above and below. Based on color photographs, the upper by Charles T. DeFrance, the lower by the author.

Feeding Behavior

Like all species of the genera *Sula* and *Morus,* the Brown Booby plunge-dives from the air into the water after its prey, chiefly fish. But unlike the North Atlantic Gannet (*M. bassanus*) or the Masked Booby, it does not usually plunge steeply into deep water from a great height. Instead it specializes in low, oblique plunge-dives and torpedo-dives at a slight angle to the surface. Inshore it often captures its prey in very shallow water, very close to the surface and near rocks, at times under rough sea conditions. Out in the ocean, where, like all other seabirds at Ascension, it must seek most of its food,

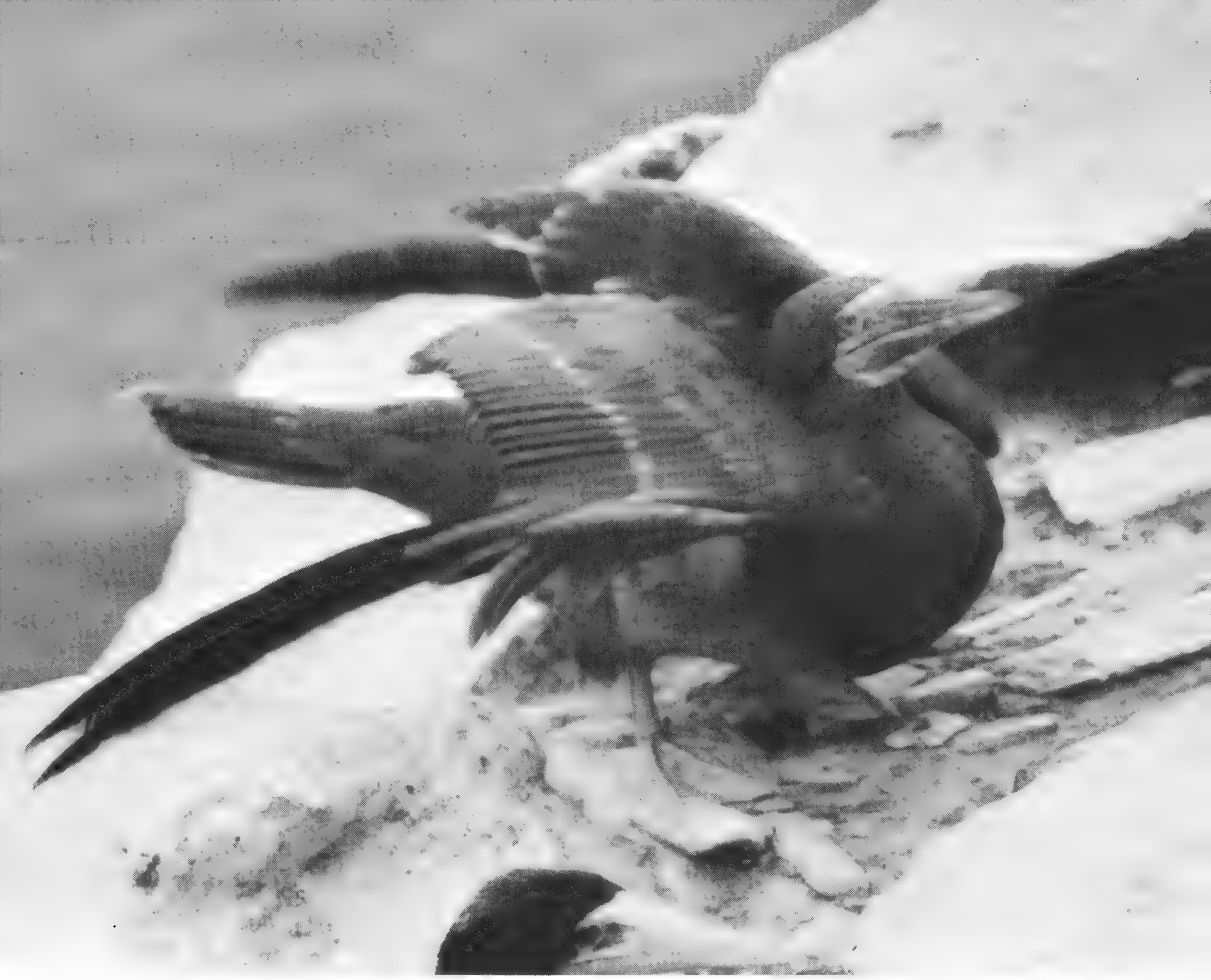


Figure 5. A returning juvenile Brown Booby Begging indirectly from the female parent. Note the wholly dark plumage. Photograph by D. F. Dorward, Boatswainbird Island.

it specializes in the aerial pursuit of flying fish (Exocoetidae)—actually capturing them in the air or, more commonly, just as they re-enter the water—and probably also habitually robs the Masked Booby of food.

I saw the Brown Boobies hunting inshore regularly in large numbers only in 1962 when there was an invasion of pelagic fish (chiefly the carangid, *Selar crumenophthalmus;* see Figure 6) that lasted for several months. For the rest of the time, inshore fishing was mostly confined to the taking of needlefish (*Scomberesox saurus*) by individual boobies. However, from time to time, minor congregations of boobies formed at small influxes of pelagic fry driven inshore by predatory fish. In April 1966, there was also some inshore fishing.

Plumage Adaptations to Feeding

In my monograph now in preparation, I argue that the anomalous dark plumage of the Brown Booby is an adaptation for "hunting-camouflage" in air-to-air and air-to-surface situations and also for "social inconspicuousness" when the individual engages, for example, in skilled fishing on dispersed prey so that it tends not to attract individuals of the same or other species which might interfere or compete with it. These selection pressures for dark plumage have overridden those for white plumage found in most other Sulidae whose white plumage is also an adaptation for hunting-camouflage (= "aggressive camouflage")—demonstrated by Phillips (1962)—but only in air-to-water situations. Further, the white plumage seems to be an adaptation for "social conspicuousness," leading to congregation at an abundant food source and cooperation, of a simple type, in exploiting it.

Population Size

Regular censuses in 1962-1964 showed some 40 adult Brown Boobies on Stack 1 and some 60 on Stack 2. These birds, mainly in pairs, were strictly residents and maintained daily contact with their home-sites throughout the year. Thirteen wore bands affixed by the BOU Expedition between December 1957 and March 1958, seven females and two males being banded as breeding birds and one female and three males as nestlings. Those banded as nestlings were now young adults and had entered the colonies between 1958 and 1962, by which time they were in their fourth year. Some of them bred between 1962 and 1964.

From other calculations I deduced that the Brown Booby at Ascension is a long-lived seabird with a small annual adult mortality—possibly as low as 3.3 per cent—and a life expectancy averaging 30 years.

Food Supply and Breeding

This low mortality among adults is the result of a basically adequate food supply that permits their own survival throughout the year coupled with a lack of natural predation both at sea and in the colony. On the other hand, conditions at Ascension are often difficult for the rearing of young and the average productivity is low.

In 1962-1964, I saw the following contrasting conditions: (1) breeding when there was an abundance of prey-fish inshore; (2) breeding when feeding conditions were average and the birds, probably feeding mainly on flying fish, engaged in moderately long oceanic trips; and (3) cessation of new breeding activity when the birds had to take longer oceanic trips in search of food. Dorward (1962a) in 1958 observed a fourth condition: a scarcity of food for a time when breeding was in progress.

While we have no direct evidence regarding the degree of abundance of surface-living prey-fish in the ocean around Ascension, indirect evidence—mainly from the seabirds nesting there—indicates that the prevailing condition is always one of food-unpredictability. The result is that the majority of seabirds have great difficulty in breeding successfully and all show a series of adaptations for breeding in this severe environment.

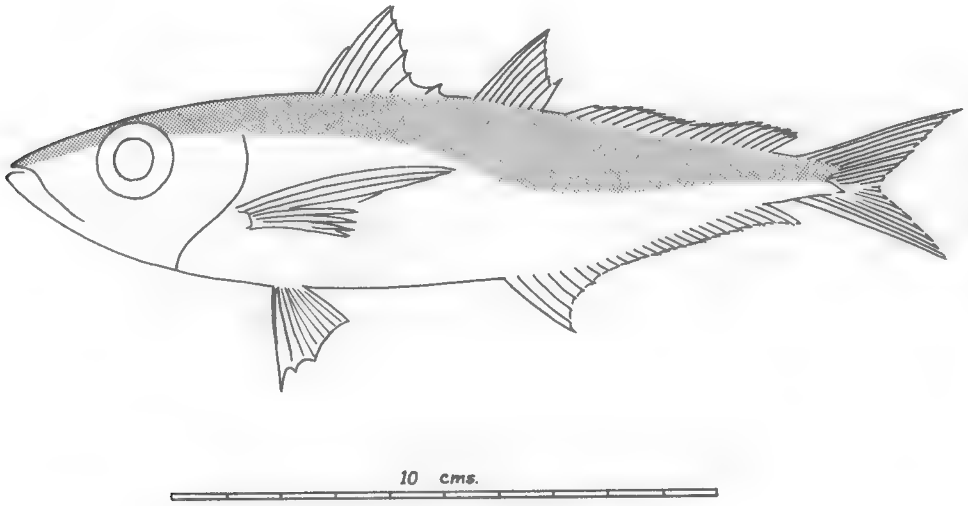


Figure 6. A pelagic fish, *Selar crumenophthalmus*. Fish of this age-class were the main prey of Brown Boobies inshore at Ascension during much of 1962. Drawing based on a field sketch by Marion Simmons, from a specimen obtained on Long Beach at Ascension, 28 July 1962.

Breeding Adaptations

I have summarized below in outline form the system of adaptations in the Brown Booby at Ascension for breeding in an environment with an unpredictable food supply.

A. ANTICIPATORY ADAPTATIONS

Adaptation	*Comment*
1. Continuous occupation of site and site "defense."	Birds maintain daily contact with their nesting territories throughout the year and show typical territorial behavior — advertisement, threat, and attack.
2. Sustained relation of pair.	Male and female maintain their "bonds" between nesting periods.
3. Conventional-periodicity.	See text.
4. Long sexual cycle.	Birds remain in breeding condition for much of the year, even when conditions for breeding are unfavorable.

B. PROXIMATE ADAPTATIONS

Adaptation	*Comment*
5. Quick response to favorable conditions.	When the food supply improves, the birds quickly go into breeding activity. Responses include a short pre-egg period of copulation and speedy ovulation, with copulation under the "control" of the female.
6. Suspension of molt.	Boobies have no well-defined molting season, but molt in a continuous sequence when not breeding, halting at whatever stage is reached when breeding is initiated.
7. Effective clutch size of one egg.	Although two eggs per clutch are normal and two eggs usually hatch, only one chick usually survives, the second chick hatched being almost invariably evicted from the nest by its sibling.
8. Second egg as "insurance egg" and second chick as "insurance chick."	See text.
9. Replacement of lost eggs and chicks when food situation continues to be favorable.	In some circumstances, replacement may be speedy (and repeated if necessary), while in unusually favorable conditions two broods may be reared consecutively.
10. Older chick capable of withstanding periods of food shortage and shows a differential growth rate.	The nestling period varied between 86 and 103 days in 1962–1964 (and may have been longer in 1957–1959), because of the current food supply.
11. Fledged juvenile returns to birth-site for long period and continues to be fed (to greater or lesser extent) by its parents.	In 1962–1964, the over-all return-period ranged from 7–59 weeks (median 23, average 25 weeks), with last feedings recorded from 6–37 weeks after fledging (median and average 17 weeks) and last sustained food-begging from 7–51 weeks (median 22, average 23 weeks). When the food supply was greater, the return-periods were shorter.
12. Parents do not nest again until the juvenile is at least independent.	This rule holds even if conditions for breeding are favorable and other birds in the colony are nesting; successful cycles last longer (mean 43 weeks) than the normal 8-month interval between the average start of successive breeding periods.

Because the species seems particularly well adapted for breeding quickly, nesting can at least begin whenever conditions are favorable, however marginally—for example, when pelagic prey-fish suddenly come inshore. There is no question that the birds time their breeding to coincide with a subsequent and predictably favorable period of available food for the rearing of young. The Brown Booby, instead of nesting according to seasons as do birds in temperate zones, starts to breed when the food supply permits the birds not only to maintain themselves, but also to sustain the cooperative routine of incubation. The outcome of the attempt is largely a matter of chance, depending on the unpredictable food supply later in the cycle. The two critical periods when most losses of eggs and chicks occur are during the six-week period of incubation and the shorter stage of early chick care when the presence of one adult at the nest is mandatory, regardless of whether the food situation is good or bad. After that, though the parents may still guard the large chick, both can go to sea simultaneously if necessary, and the losses of chicks from starvation are fewer.

Periodicity of Breeding

The "anticipatory" adaptations (see summary outline, above) ensure that Brown Boobies are ready to breed, on the average, more or less at any time of year. One adaptation, "conventional-periodicity," is a new concept. Dorward (1962a) suggested that the Brown Booby has a less than annual—an eight-month—periodicity, breeding near April and December one year and in August the next. I confirmed this eight-month system with some modifications: While an intrinsic, physiological rhythm brings the birds to the peak of breeding condition about every eight months, the current food situation actually determines the start of breeding; and, if the food conditions are particularly favorable, the breeding season may even be prolonged.

There is no evidence that the eight-month periodicity coincides with any optimal regular supply of food. On the contrary, as far as environmental factors are concerned, it is basically *arbitrary*—thus the qualification "conventional." This periodicity ensures that the birds are in breeding condition as often as possible, less than annually, so that they stand a better chance of "hitting" the irregularly occurring, favorable periods of available food than if the cycle were annual.

The timing mechanism determining the eight-month "calendar" of the Brown Booby at seasonless Ascension is obscure, and, as Miss P. A. Butterfield points out, the physiological problems imposed by this regime are considerable. Simmons (1965) has indicated that the eight-month periodicity marshalls the breeding attempts of the unsuccessful nesters of the previous breeding period more quickly than in an annual cycle. Such birds are in the majority, the cycles of the fewer successful breeders taking appreciably longer than eight months to complete on the average. This is because the young birds fly in and out of the colony for a long period following fledging and beg food from their parents (Figure 5).

At Ascension, the extreme example of conventional-periodicity is observed in the Sooty Tern (*Sterna fuscata*) which starts nesting at an average interval of 9.6 months (Chapin, 1954; Ashmole, 1963), entirely non-seasonally. However, unlike the Brown Booby, the tern progresses inexorably from laying period to laying period apparently regardless of the local food situation. This may be because of the remoteness of its feeding grounds. As a result, some of its nesting attempts are almost totally disastrous. Even more than in the Brown Booby, the conventional-periodicity of the Sooty Tern is an adaptation, not to breeding at the optimum time, but to breeding at all (Simmons, 1965). The synchronization of laying seems basically intrinsic and, as pointed out by Ashmole (1963), an adaptation in the past to the bird's need to reduce predation of chicks by Ascension Frigate-birds (*Fregata aquila*). In most other Ascension seabirds, however, including the Brown Booby, actual synchronization is of no advantage *per se* but indicates the common response of the population to a favorable food supply.

Clutch Size

Following the initiation of breeding, the "proximate" adaptations start to operate (see summary outline, above), ensuring that egg-laying quickly follows and that every chance is afforded for the survival of the chick in the rigorous conditions at Ascension. One of these adaptations needs special comment. Murphy (1936), Wynne-Edwards (1962), Nelson (1966b), and Lack (1966) have discussed the fact that this species, as well as its pantropical congener, the Masked Booby, has an anomalous clutch of two eggs even though only a single chick, if any, is usually reared. Dorward (1962a) states that only a single chick is reared regardless of the food supply and suggests that the second egg, laid some five days after the first, functions "as insurance against loss of one during incubation," a view not generally accepted.

While I believe that Dorward is basically correct, we should consider this "insurance" egg in a broader context as part of the system of adaptations: If the first egg is lost before the second is produced or either egg lost later, then the breeding attempt can proceed with little or no interruption and with no need to restart the whole process. An even greater advantage occurs if the first-born chick dies before the second has hatched or been destroyed. The second chick becomes the insurance chick and permits the cycle to continue. In both cases the maximum use of a favorable food supply is assured.

Some Determinants of Social Behavior in the Brown Booby

I use the term "social behavior" to describe interactions between conspecific individuals, involving communication through postures, movements, and calls. The Brown Booby has an extensive repertory of social behavior and, while some behavior patterns are highly ritualized (stereotyped with a "typical intensity"), others are "fluid" with their components less well differentiated. I sketch this repertory briefly, aided by illustrations, and with particular reference to some of the important determinants of social behavior in this species.

Selection favored a permanent site-tenacity among Brown Boobies at Ascension — and probably elsewhere at blue-water stations with similar environment—as an anticipatory adaptation for quick breeding in response to irregular improvements in the food supply. This necessitated the development of strong, persistent, and ritualized aggressive behavior toward other site-contending boobies, actual or potential. At the same time two trends—one toward "*spaced*" nesting and the other toward "*steep*" nesting—influenced the present form of behavior.

All evidence suggests that the Brown Booby, like most other boobies (*Sula* spp.) but unlike the gannets (*Morus* spp.), is not typically a dense nester. At some stations, as on Christmas Island in the Indian Ocean (Gibson-Hill, 1947), isolated nests and small groups of nests are common. When the Brown Booby does form colonies, the nest-sites are usually some yards apart, with the birds well beyond range of their neighbors' bills. Of course, much depends on the local situation. A shortage of sites may result in a greater density of nests

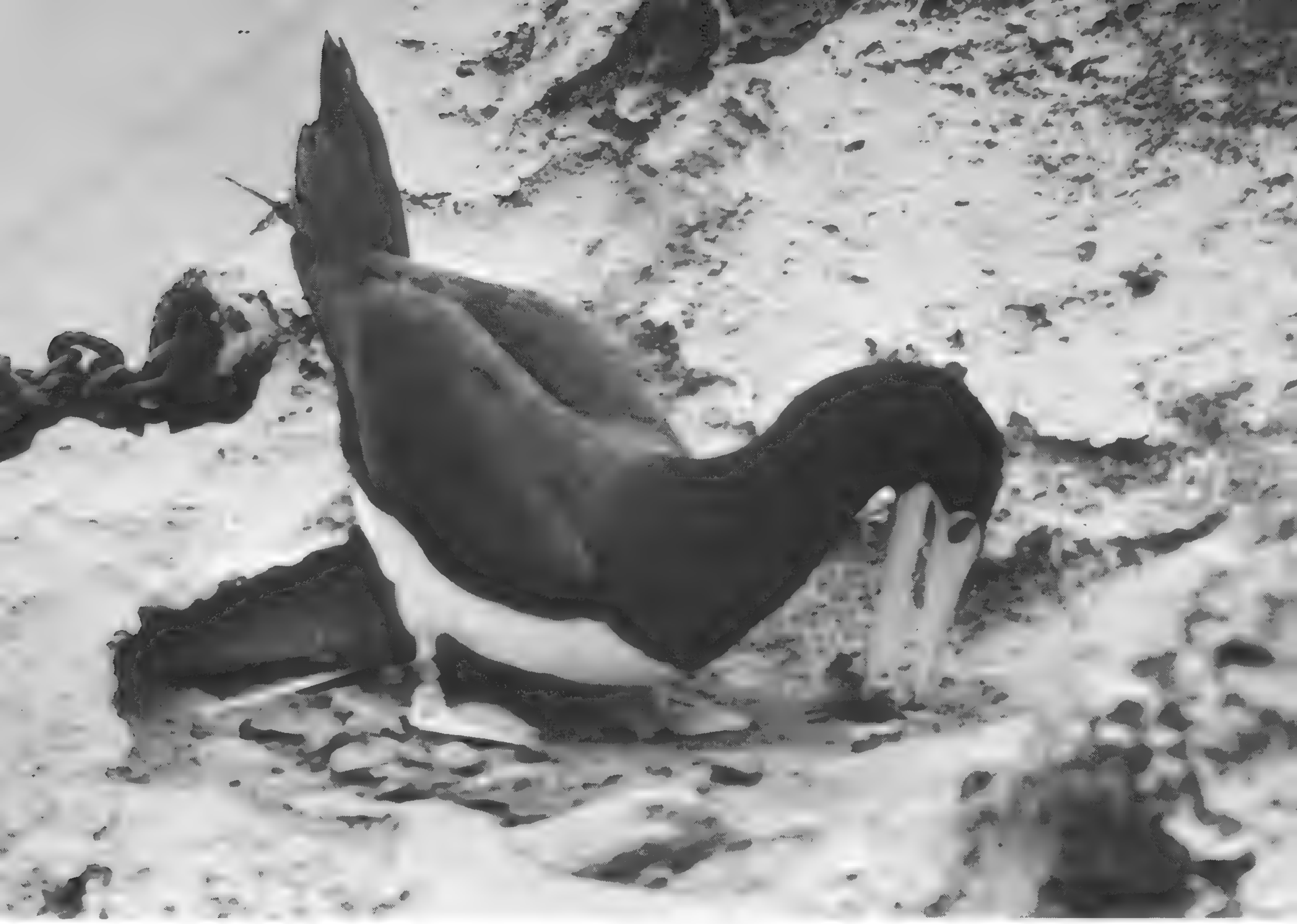
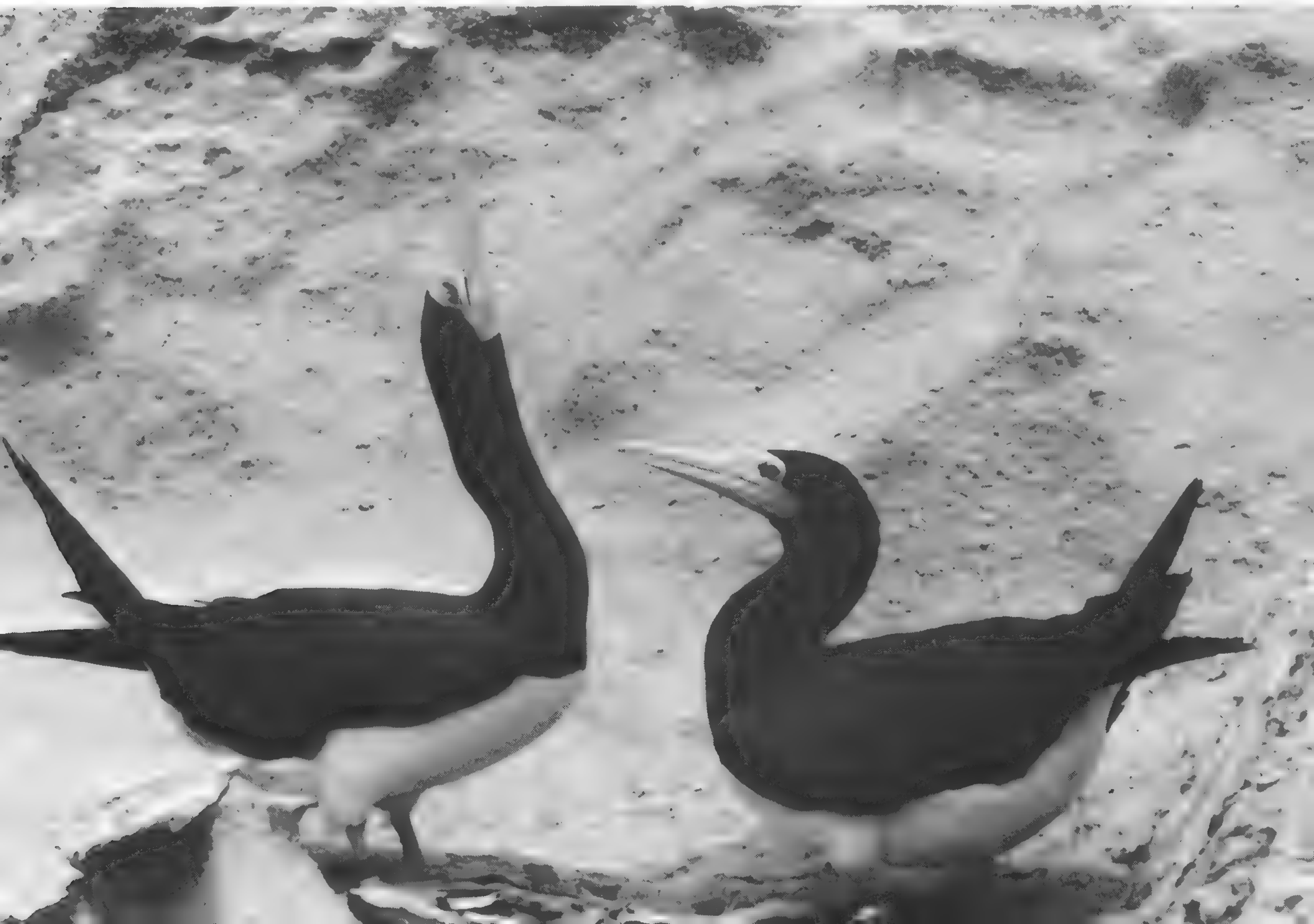


Figure 7 (*above*). A female Brown Booby in a nest-hollow. Here, at the lower phase of the Bow, she is calling and mandibulating nesting material. Photograph by D. F. Dorward, Boatswainbird Island.

Figure 8 (*below*). A male Brown Booby Saluting the female in the nest-hollow. Note the alignment of eyes between the sexes and the species-specific posture of the male, with head Thrown-back in the Sky-point and the lack of any wing movement. Photograph by D. F. Dorward, Boatswainbird Island.



and this is partly the case on the five stacks at Ascension where the birds can no longer use the mainland sites. But even on these stacks I found no really dense nesting and where a few nests were close together, their distribution was linear, with no encirclement by other nests as in colonies of gannets and some other boobies. A typical nesting territory of a pair of Brown Boobies is not restricted to the nest-site itself. The birds perch on vantage points around the nest and on auxiliary perches away from the vicinity of the true nesting territory—often on more or less sheer spots on cliff faces.

This dispersal of nests is a species-specific character that evolved because dense nesting is normally of no advantage to the Brown Booby, breeding as it does on islands that have no serious natural predators and with no need to synchronize its laying either to reduce predation on eggs and young or to take advantage of a seasonal food supply. In fact, dense nesting and a concentration of birds on any one stretch of coast might be a distinct disadvantage to the Brown Booby, specialized as it is in skilled, individual, inshore fishing. In this species, as in most other boobies, a density of nests indicates a shortage of suitable nesting sites.

In addition to spacing its nests, the Brown Booby also characteristically chooses "steep" sites for nesting and perching. These are slopes, rocks, the tops, and even faces of cliffs on the periphery of islands overlooking the sea. Before man came to Ascension, the species probably nested linearly, singly, and in spaced groups on the headlands and cliffs of the mainland, as it does today on Boatswainbird Island (Dorward, 1962a; pers. observ.) where there is apparently no shortage of the sites it prefers.

The influence of spaced nests and steep sites on the Brown Booby's social behavior is extensive — especially on its antagonistic repertory. In the first place, the Brown Booby, unlike the boobies that nest on flat ground, is unrestrained by close neighbors and can readily take wing from a vantage point. In the following account I have capitalized clear-cut behaviors, whether ritualized or not.

Antagonistic Behavior

In antagonistic behavior the emphasis is on aerial activity. Birds engage in aerial Reconnaissance over neighboring sites, at times performing special Provoking-flights by repeatedly dipping low over, for example, a disputed site with a Chin-bracing movement. Site-owners commonly chase intruders for some distance in Flight-pursuit and there is a ritualized "fight" in the air, the Rise-and-fall, which ceremonially ends such an encounter.

Attacks, too, may be made from the air and the steep nature of the site obviously determines their form. Intruders are frequently Supplanted when the site-owner flies in, calling persistently, and either perches near the intruder, causing it to flee (Indirect-supplanting), or actually lands in its place as it flies off (Direct-supplanting). In cases of persistent intrusion, especially by sexual rivals, the site-owner sometimes Torpedo-attacks its adversary from the air, plunging down on it in a shallow trajectory with wings thrown back as if plunge-diving for food, crashing on it, and seizing it by the bill. Ground fights (true Combat) involve the gripping of the rival's bill, head, or neck and pushing against it while advancing with extended neck (Pressing) so as to force it over the edge and thus dislodge it.

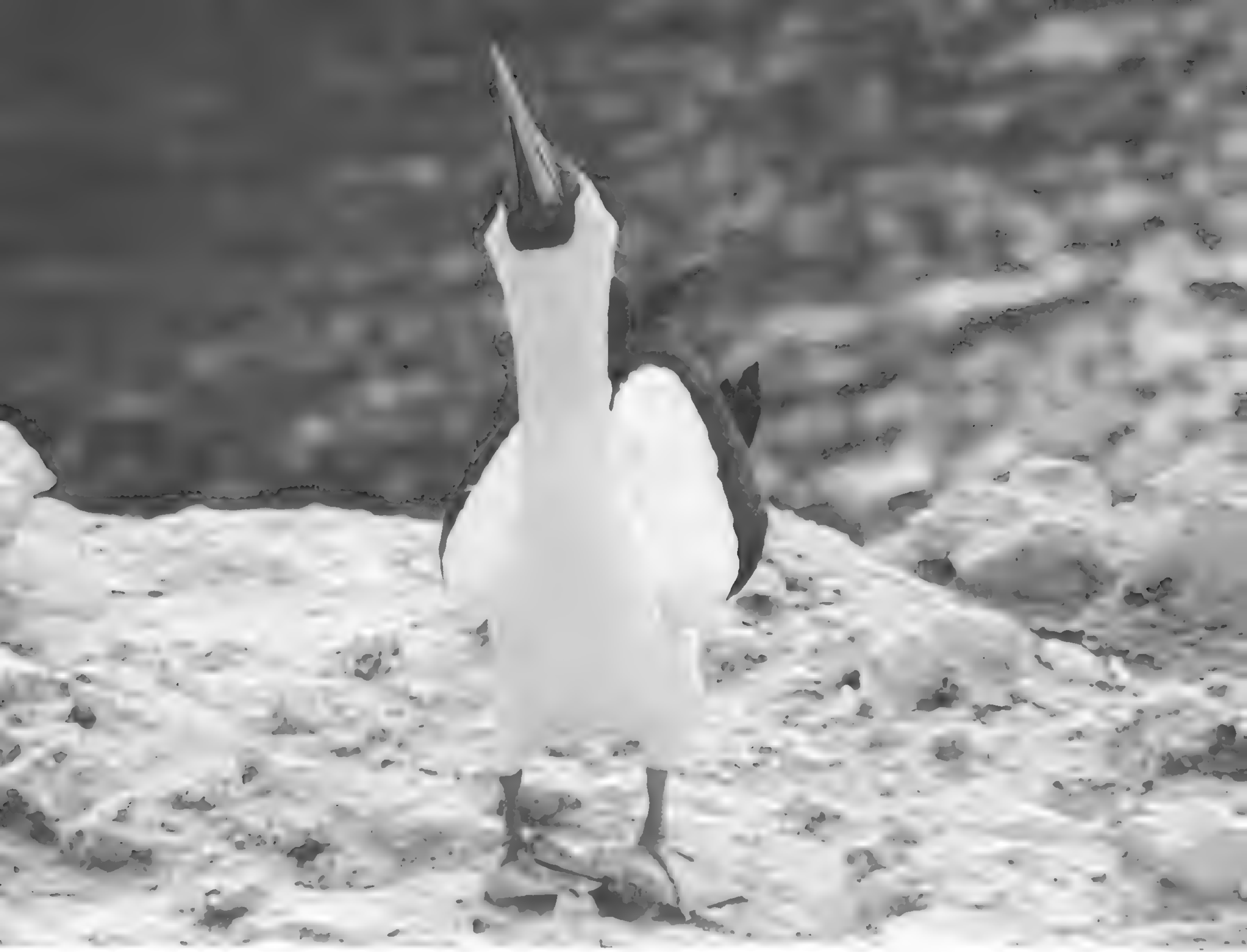
Other behaviors have evolved especially to force an intruder, when it lands near the nest-site, to flee quickly in alarm without Combat. The most elaborate of these are the Wings-up display and Darting whereby the nesting bird—particularly the one in charge of eggs or chick liable to be harmed by fighting—suddenly flicks up its wings and jumps forward at the intruder with extended neck and pointing bill, a behavior most effective in driving birds from steep sites. (This same situation has been exploited by the older chick, whose activities are not otherwise considered here, when it thrusts toward the intruder uttering a frightening sound—the Roar.)

One of the main "site-proclaiming" behavior patterns in the Sulidae occurs more or less invariably when a site-owner of either sex lands at its site. This consists of landing-calls and a post-landing display (van Tets, 1965; Nelson, 1965). In the Brown Booby the Landing-calls are well developed, but the post-landing display is lacking. Presumably, spaced nesting has resulted in more emphasis on the vocal component which is more effective at a distance than the visual one. Similarly, the Site-ownership display, so prominent in gannet behavior (Nelson, 1965), is not very elaborate in the Brown Booby. It consists mainly of Bowing (Figure 7) exaggeratedly toward the ground while calling (see description below, under sexual behavior). This display, derived from nest-arranging movements, has a wide range of intensity in most situations. In one particular situation — when flying intruders pass near the site — it is normally given at high intensity. Bowing then consists of a marked head-dipping and head-raising sequence while the bird calls persistently, sometimes raising and "showing" nest-material in the bill, as well as redirecting its aggression to the material. The redirected activity, not particularly well developed in the Brown Booby, is called Nest-worrying by van Tets or Nest-biting by Nelson.

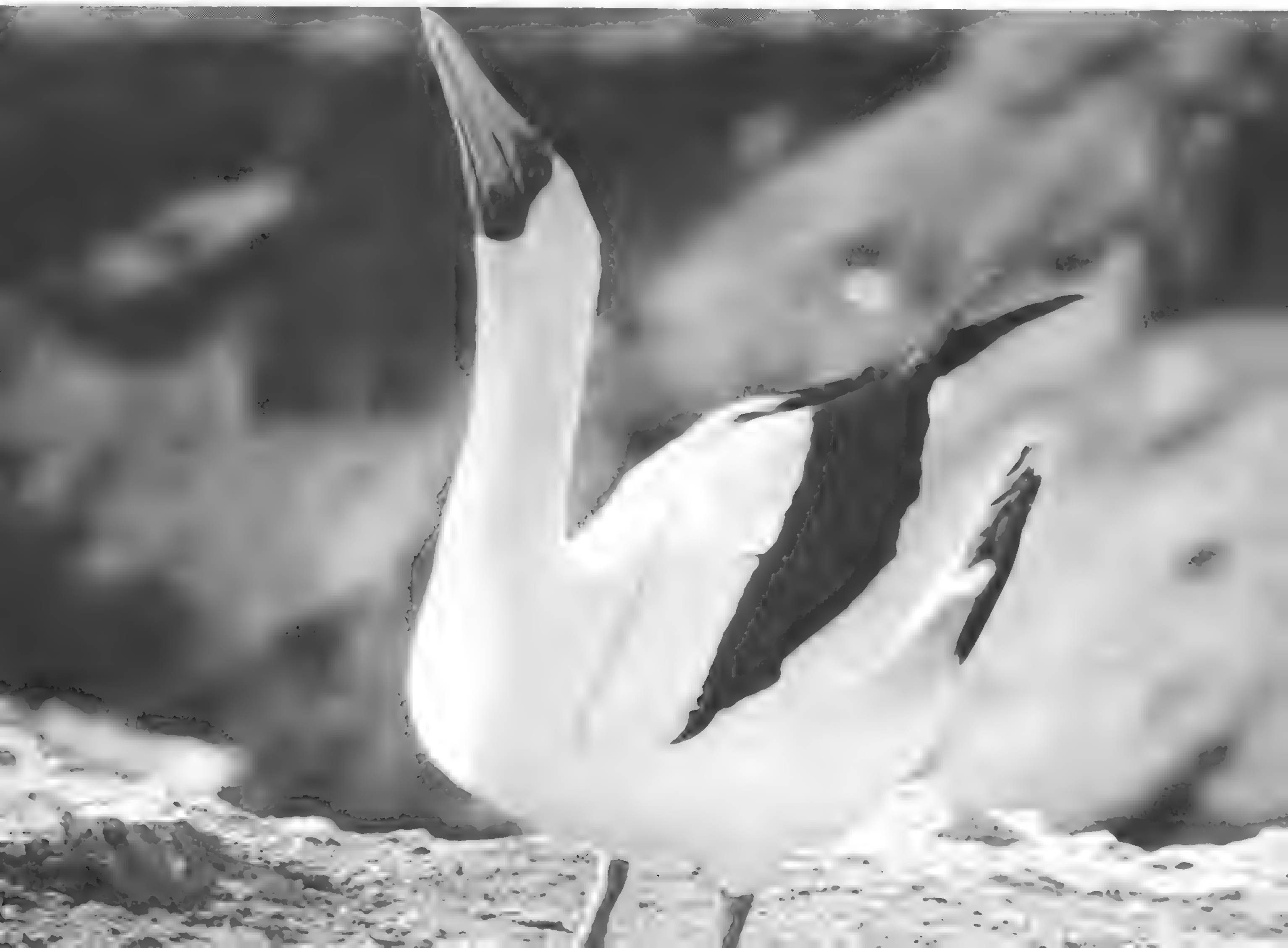
As a further consequence of spaced nesting the close-quarter antagonistic behavior, that falls short of actual Combat, is not well differentiated. It consists mainly of Ruffling the feathers, particularly those of the head, and an unritualized Lunging of the bill toward the opponent. This at times develops into a mutual Jabbing bout. Some individuals show basically the same behavior to the human intruder at the nest. In the Brown Booby there is no elaborate stationary threat-display of the "Menacing" type found in the North Atlantic Gannet (Nelson, 1965) or the "Head-wagging" behavior characteristic of aggressive encounters in some boobies — for example, in the Masked Booby (Dorward, 1962b).

While the Brown Booby is generally aggressive, it is not as "hyper-aggressive" as the North Atlantic Gannet (Nelson, 1965; 1966a) in which the males particularly show great pugnacity, especially when establishing pair-bonds and nest-sites in densely crowded colonies. Similar pressures of seasonality and dense nesting are less acute with the Brown Booby at Ascension.

In the Brown Booby the premium is placed on the evolution of any adaptation that facilitates quick responses, enabling breeding to start when conditions are favorable. This has produced a system in which the sustained possession of a mate and a nest-site are of great and equal importance—particularly, it would seem, to the female. Disputes over mates and sites are more intense between the more aggressive females than between the males. The female Brown Booby "defends" the nesting territory even more effectively than the male; she dominates the scene with her louder calls. Unpaired females sometimes establish sites which males visit as well as *vice versa*. This "emancipation" of the female probably arose because of her important role in producing eggs after speedy ovulation, which is the first stage in the series of proximate adaptations for quick breeding. The female's role also requires her to be the dominant partner in copulation (see below) so that fertilization and the timing of the breeding attempt at a critical period is strictly under her control.



Figures 9 (*above*) and 10 (*below*). Two views of a male Masked Booby Saluting a distant female. Note the Wings-up posture of this species. The frontal view shows well how the male maintains his binocular stare from "under" the bill while Sky-pointing. Photographs by J. M. Cullen, BOU Centenary Expedition, 1957-1959, Boatswainbird Island.



Sexual Behavior

In the Brown Booby aggressive behavior over mates and territory "overflows" into the relationship between male and female, resulting in an undercurrent of strong agonistic tendencies, especially at the nest-site where territorial aggression is strongest. This condition appears commonly in some other birds—for example, the Herring Gull (*Larus argentatus*) (Tinbergen, 1952), Great Crested Grebe (*Podiceps cristatus*) (Simmons, 1955), and North Atlantic Gannet (Nelson, 1965). However, unlike the grebe in which sexual behavior (used in this paper to cover all intersexual activities involving birds of the opposite sex that are in the process of establishing sexual bonds or maintaining them) is extremely ritualized and arranged in stereotyped sequences or "ceremonies" without any overt aggressiveness, the booby's agonistic tendencies lie "at the surface" and often find direct expression during sexual interaction. Further, the greater overt aggressiveness of the female Brown Booby affects the relationship between the sexes. The male tends to show a greater escape element in his sexual behavior and to be more "defensive" and "nervous."

These agonistic tendencies not only affect the present motivational basis of sexual behavior but also have had an important influence on the evolution of much of its form. We are not surprised, therefore, to find that there are special activities characteristic of critical situations at or near the nest-site. These include behavior performed: (1) *at a distance* from the partner, out of contact-range, either before or after close interaction, the most differentiated behavior confined to the male—Saluting; (2) *at the meeting* of the male and female, when they come within contact-range after a separation—Bill-pointing, Bill-touching, Symbolic-feeding; (3) *at sustained close proximity,* when male and female remain together—Billing, Sparring; and (4) *during moving away* from the partner—Parading, Bill-up, Bill-tuck, Face-away. I use the term partner here to include not only the "true" mate but also any individual of the opposite sex involved in the process of pairing-up or any bird, paired or unpaired, associating with the paired birds. In addition to the above behaviors and situations, the environmental factors—spaced and steep nesting—so important in determining the form of antagonistic behavior, also influence sexual behavior; for example, aerial activity is common.

At a Distance

When male and female are positioned in the nesting territory, yet beyond contact-range, either, or both, may Bow at a partner (Figure 7). Bowing is a characteristic, moderately differentiated "distance" reaction, especially of the "in-bird"—the bird standing or sitting in the nest-hollow. The bird looks at its partner and then lowers its head close to the body with bill pointed vertically downward either to or near the ground in a full Bow, or only towards the ground in a partial Bow (a Dip). The bird sometimes Bows frontally (Front-bowing), but more commonly the bill extends either by the side of the breast (Side-bowing) or near the ventral flanks (Backward-bowing). It may also mandibulate nest material, if present, or briefly preen at the flank or wing feathers.

Bowing, though occurring anywhere when one partner moves away from the other or acts as an "intruder," commonly begins at the nest-site. In the intruder situation, the in-bird Bows when its partner flies into the territory and perches outside contact-range without engaging in the formal Greeting behavior (see below). Sexual Bowing is clearly homologous with and closely

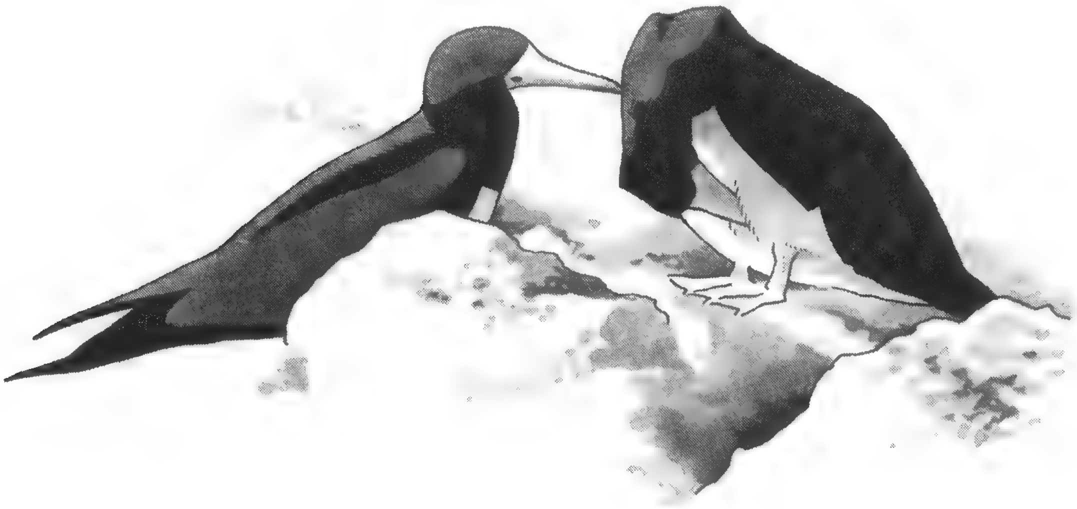


Figure 11. Allo-preening by the Brown Booby. The male is Nibble-preening the female's neck while she is self-preening her breast. Based on a color photograph by the author, Stack 2, 17 February 1964.

resembles antagonistic Bowing, especially in its less intense forms when both behaviors tend to degenerate into more or less functional Nest-arranging. However, the sexual Bowing, usually of lower intensity, is often modified by personal recognition and bonds as well as by appeasing elements (see below); the birds are either silent or call to the partner less vehemently than in antagonistic situations.

In the male Brown Booby especially, sexual Bowing is typically prefaced by Staring—the bird gazes with a fixed, binocular stare, or "intent-look," directly at the partner. Often it first stretches its neck upward in a deliberate manner—the Stretch-up-and-stare. The booby holds this posture until some movement from the partner initiates Bowing. It is here, in this situation, that Bowing behavior probably functions as a pair-bond display of the "nest-showing" type (van Tets, 1965).

However, the Stretch-up-and-stare is even more typically the first phase in a male-specific and highly differentiated display, Saluting (Figure 8). Uttering a disyllabic Wheeze-whistle, the male quickly throws up his head, the Throw-back, and briefly holds it vertically, Sky-pointing, thus showing the chrome-yellow of his gular area to the female while continuing his bittern-like stare now from under the bill. This display shows little variation in intensity under different situations, but the amplitude of the Throw-back depends on the position of the female. The frequency and timing of the Salutes in a given sequence depend on whether or not the male has secured her gaze; for, at least when she is perched, he does not Salute her unless she looks at him, however fleetingly.

Although there is little variation in the form of Saluting, the Wheeze-whistles of neighboring males differ mainly in quality and degree of stress on the component syllables. As these differences are obvious to the human observer, the female booby very likely distinguishes individual males by the same means. Dorward (1962b) described this behavior as an advertising display in the Brown and Masked Boobies at Ascension and named it Sky-pointing. I had independently called it Saluting after the name given by Richdale (1951) for a superficially similar behavior pattern in the Yellow-eyed Penguin (*Megadyptes antipodes*). I prefer to retain this general term while restricting Sky-pointing specifically to the vertical head and neck posture. The Saluting of the Brown Booby differs from that of all four of the other common boobies, the Masked, Red-footed, Blue-footed (*Sula nebouxii*), and Peruvian (*S. variegata*), in that its Throw-back and Sky-point are not accompanied by Wing-up posture (Figures 9 and 10). This behavior in the rare *Sula abbotti* is as yet unknown. Also, the male Brown Booby seems to be the only one that commonly performs Aerial-salutes in the vicinity of the nesting territory, in which he soars briefly in a graceful, upward "swallow-glide" while Throwing-back and calling.

Saluting in the Brown Booby is most usually given by: (1) a lone male, paired or unpaired, to a female perched outside or flying over his nest-territory; (2) a male whose partner is within the nesting territory but perched apart from him (either bird can be the in-bird—though it is more frequently the male); (3) a male when his partner moves away from him, especially when he is the in-bird; and (4) a male in flight behind and above a female when, as they Fly-together synchronously, he often seems to be trying to steer her back to his nest-territory.

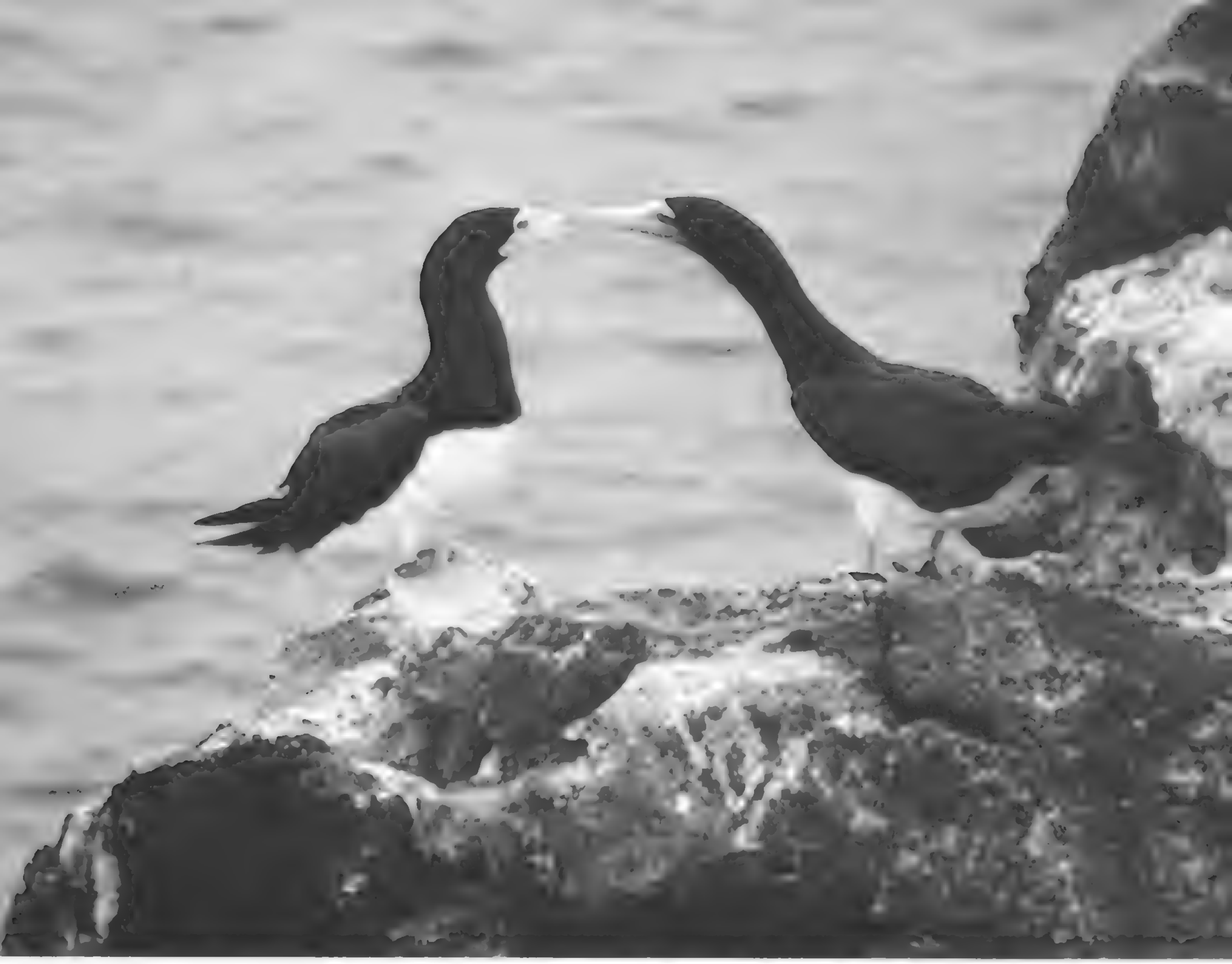
In many cases, Saluting is clearly an advertisement display whereby the male initially attracts a female to him, or causes his partner to rejoin him, especially at the nest-site. In the Masked Booby, Saluting ceases when the female joins the mate (Dorward, 1962b), but in the Brown Booby (as Dorward also noticed) Saluting frequently occurs when the male and female are together at the nest-site. This suggests a more extended function of Saluting in maintaining the pair bond and as an appeasement display, particularly in fully paired birds.

Sometimes, the male Brown Booby Salutes the female when they are within contact-range and largely quiescent, often for no apparent reason, but occasionally in direct response to some hostile bill-action on her part. Further, in most or all other boobies (particularly the Blue-footed, Red-footed, and Peruvian) both sexes may Salute either simultaneously or alternatively. But, in the Brown Booby, I have never once recorded a female Saluting in any circumstance. This underlines the importance of the display to the male Brown Booby, undoubtedly as appeasing behavior to the larger, more aggressive female. Finally, in true pairs of this species, Saluting is essentially a pre-egg activity and hence probably sexually stimulating to the female, though it is not, strictly speaking, a precopulatory display (see below).

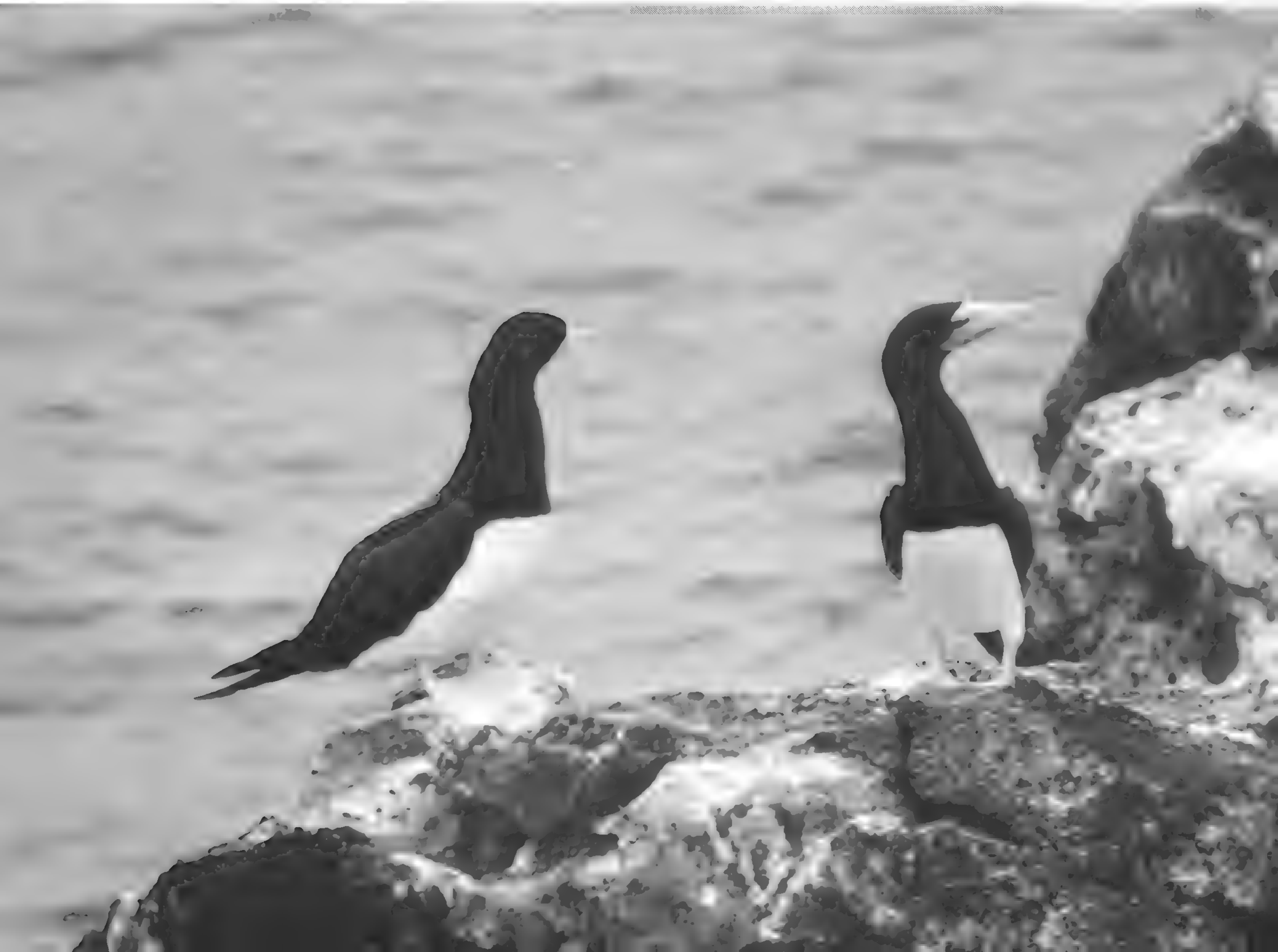
At the Meeting and Close Proximity

Much of the rest of the sexual behavior of the Brown Booby is mutual and involves the bill, the offensive weapon in the Brown Booby and also the main target for attack during close fights and disputes between rivals. The dynamic frontal presentation of the bill to another bird, even a passive frontal showing, indicates potential hostility as well as provoking attack. It is not surprising, therefore, that various attack-reducing activities have evolved in sexual situations, especially when male and female are within contact-range of each other; and that such activities involve both the mutual engagement of bills and its converse, the averting of bills.

When together on the ground and facing each other, the pair frequently engage in Billing activities (Figure 22). These are various "friendly" movements in which the birds, usually without obvious signs of overt aggression, touch, nuzzle, and nibble each other's bill and facial skin, often simultaneously or reciprocally but sometimes unilaterally—in the latter case more often by the male. Billing seems to be this species' equivalent of the marked Allo-preening (Cullen, 1963) of most other Sulidae, which, as a sexual activity, is uncommon and undifferentiated in the Brown Booby, although individual



Figures 12 (*above*) and 13 (*below*). Two views of a male Brown Booby (right) Bill-pointing with a female, then turning away in the Bill-up-face-away posture with the Neck-twist moderately intensified. Photographs by the author, Stack 1, 16 February 1964.



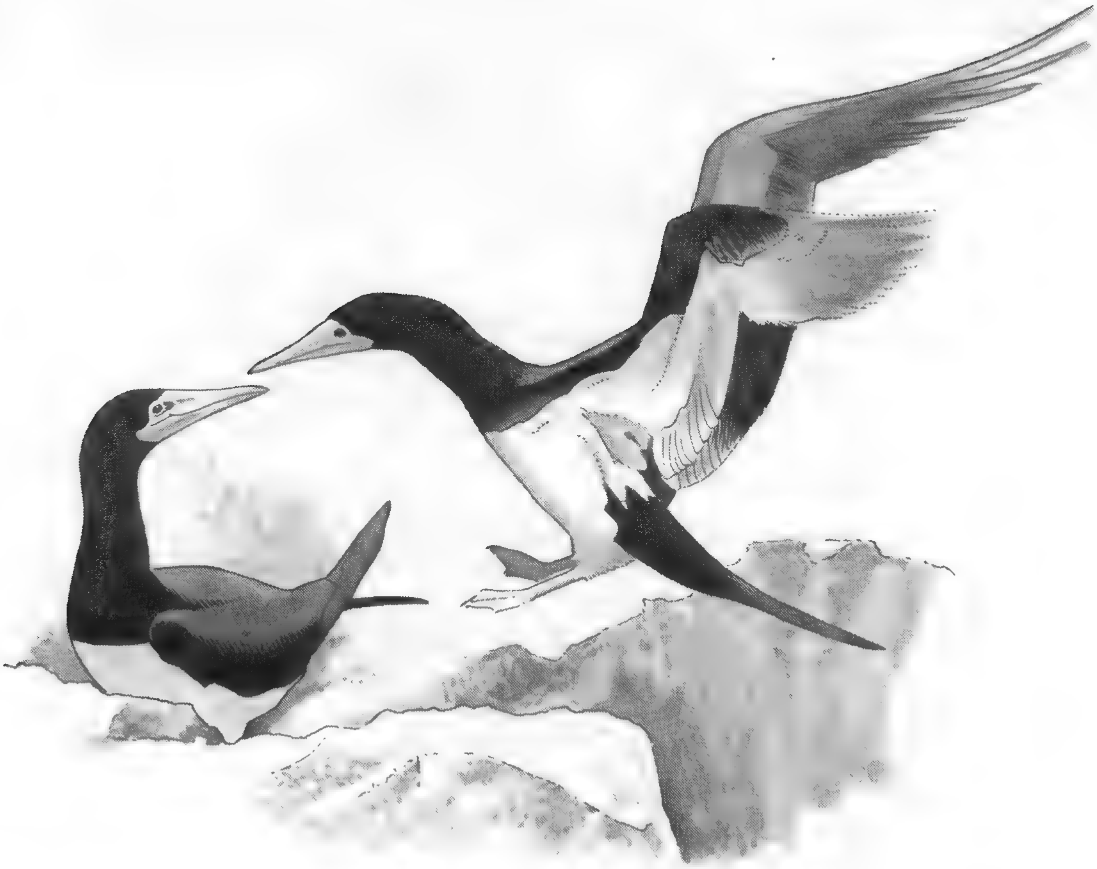
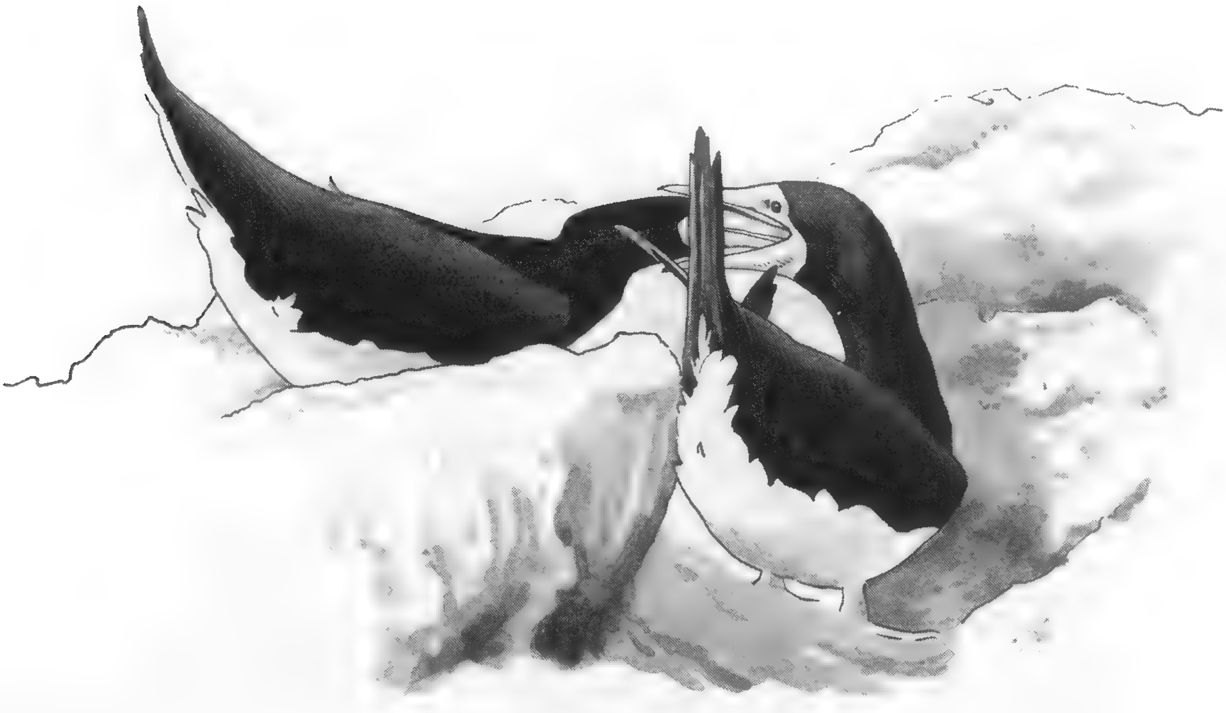


Figure 14 (*above*). Greeting-ceremony of the Brown Booby, the male landing. Based on a color photograph by the author, Stack 1, 27 January 1963.

Figure 15 (*below*). Symbolic-feeding of the Brown Booby. The male is inserting his bill within the throat of the female. In this instance, he is assuming the "chick role." From a color photograph by the author, Stack 2, 19 February 1964.



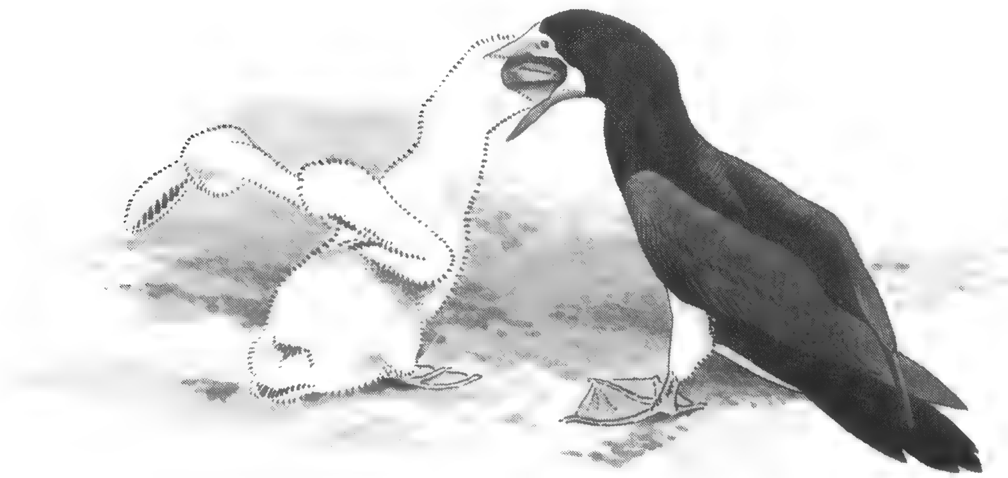


Figure 16. A chick taking food from the parent female Brown Booby. Compare with Figure 15. Based on a photograph by J. M. Cullen.

males may occasionally Nibble-preen the mate's feathered parts of the head while she is inactive or busy preening herself (Figure 11). Parents of both sexes regularly preen the downy chick. Equally common with Billing are the Sparring activities, obviously hostile movements in which the birds poke or fence with each other's bill, though never as committedly as in true bill-fighting in antagonistic situations. The aggression here is inhibited and also ritualized to some extent, particularly in one highly characteristic activity, called Bill-pushing by Dorward (1962b). In this behavior, one bird pushes forward with its bill while the other pulls its head well back, usually with a quick reversal of roles that results in a rapid see-saw sequence. As Dorward also noted, Pushing is chiefly a movement of the neck, the two birds moving "as if to probe each other in the eye." Ordinary Billing often degenerates suddenly into Sparring, which seems to occur simultaneously in both birds but usually is caused by some provoking movement by only one bird—frequently a hostile act from the female, but also an "anticipatory," defensive one from the more nervous male. In other instances, the transition between Billing and Sparring is less clear cut.

Bouts of Billing and Sparring usually begin by Bill-pointing (Figures 12 and 14) in which one bird directs its bill formally towards the tip of its partner's bill. The second bird usually responds immediately with similar behavior resulting in mutual Bill-touching. Bill-pointing has special relevance when one bird rejoins its partner. Return to the site is especially provocative to both sexes in this aggressive species. They take part in a stereotyped Greeting-ceremony that obviously evolved to sublimate their territorial hostility by "immobilizing" the bills. The returning bird flies in, giving typical, sex-specific Landing-calls and aligning its bill for Bill-touching while still in the air (Figure 14). The ground-bird, also calling, makes similar preparations so that, at the very moment of landing, the two are in formal bill-contact with the tips opposed in a "frozen" greeting. Should the returning bird not land close to its partner, it then walks or jumps in close while Pointing with the other bird. Billing and other activities follow, including one behavior which seems to be confined to the male, Symbolic-feeding or "Allo-feeding" (Figure 15). Occasionally, after Bill-pointing, the male booby encases the female's bill in his or inserts his bill well into her mouth, making "token" shoveling movements as if either feeding or taking food from her, as in parent-chick situations (Figure 16). However, no food is ever passed and the female's role is quite passive. I observed Allo-feeding behavior mainly in newly formed or pairing couples, whereas I saw the rarer Allo-preening in long-established pairs.

During bouts of Billing and, especially, of Sparring, various Bill-averting actions occur. The simplest of these is Bill-shaking which is the same in form as the common comfort-movement but is different in frequency and initiation. The main activities, however, involve the lowering, raising, and turning away of the bill, particularly in direct response to hostile actions by the partner. Though common to both sexes, these activities are especially characteristic of the male. There is a wide range of more or less undifferentiated intensity variants which grade into one another during fluid sequences of relatively mild bill-action and reaction, but once the Sparring of one bird becomes more forceful, the other tends to avert its bill in a much more ceremonial manner by assuming one or more of the following postures: the Bill-tuck (Figure 17), the Bill-up (Figure 13), and the Face-away (Figure 13). To some extent, also, these postures have been "emancipated" from their immediate eliciting stimuli during sequences of sexual behavior, especially in the male.

In the full Bill-tuck, the bird arches its neck and lowers the bill so that it presses against the jugulum; in the Bill-up, it tips the head back and, with neck more or less erect, points the bill skywards; while in the Face-away, it turns the bill right away so that the back of its head is presented to the partner. Throughout, the bird that is Bill-averting keeps glancing at the other, so there is no question that the postures function in "cutting off" the aggression by one bird (Chance, 1962). The full Bill-tuck is a static, entrenched posture but in the others the bird moves away from the partner; for example, when one bird forcibly Spars with it, the other bird Faces-away, then turns, and walks off.

During Moving Away

When walking in the vicinity of the partner, the moving bird often Parades (Figure 17) formally with a mincing, "Pussy-footing" gait, neck held erect and tail cocked. When Parading away from the partner while within contact-range—and especially on leaving it in the nest-hollow after Sparring—the bird is then most likely to Face-away as it goes, with the bill more often raised or lowered than held straight, and often with a Neck-twist as it turns its head to one side so as to "keep an eye" on the partner. During Parading, the high intensity Bill-up posture is often combined with Facing-away to produce the distinctive Bill-up-face-away, first described and named by Dorward (1962b). However, it must be made absolutely clear that this display is typically correlated with movement on foot away from the partner and not with movement towards it, as Dorward claimed, while other combinations are equally typical of Parading, especially Bill-down-face-away. As a rule, an upward orientation of the bill in the Brown Booby indicates that the Parading bird may hop, flutter, or fly away, while a downward orientation conveys the opposite. Thus, Parading in the extreme Bill-up posture is a common Preflight display in social (agonistic) situations, the departing bird often taking wing to circle and land again at the site where it usually rejoins its partner and performs the Greeting-ceremony with it. Conversely, Parading is often terminated ceremonially by hopping or fluttering up or down to a perch nearby and landing with a marked Bill-tuck (Figure 17) — a characteristic pelicaniform Hop-display in the sense of van Tets (1965). All these Bill-

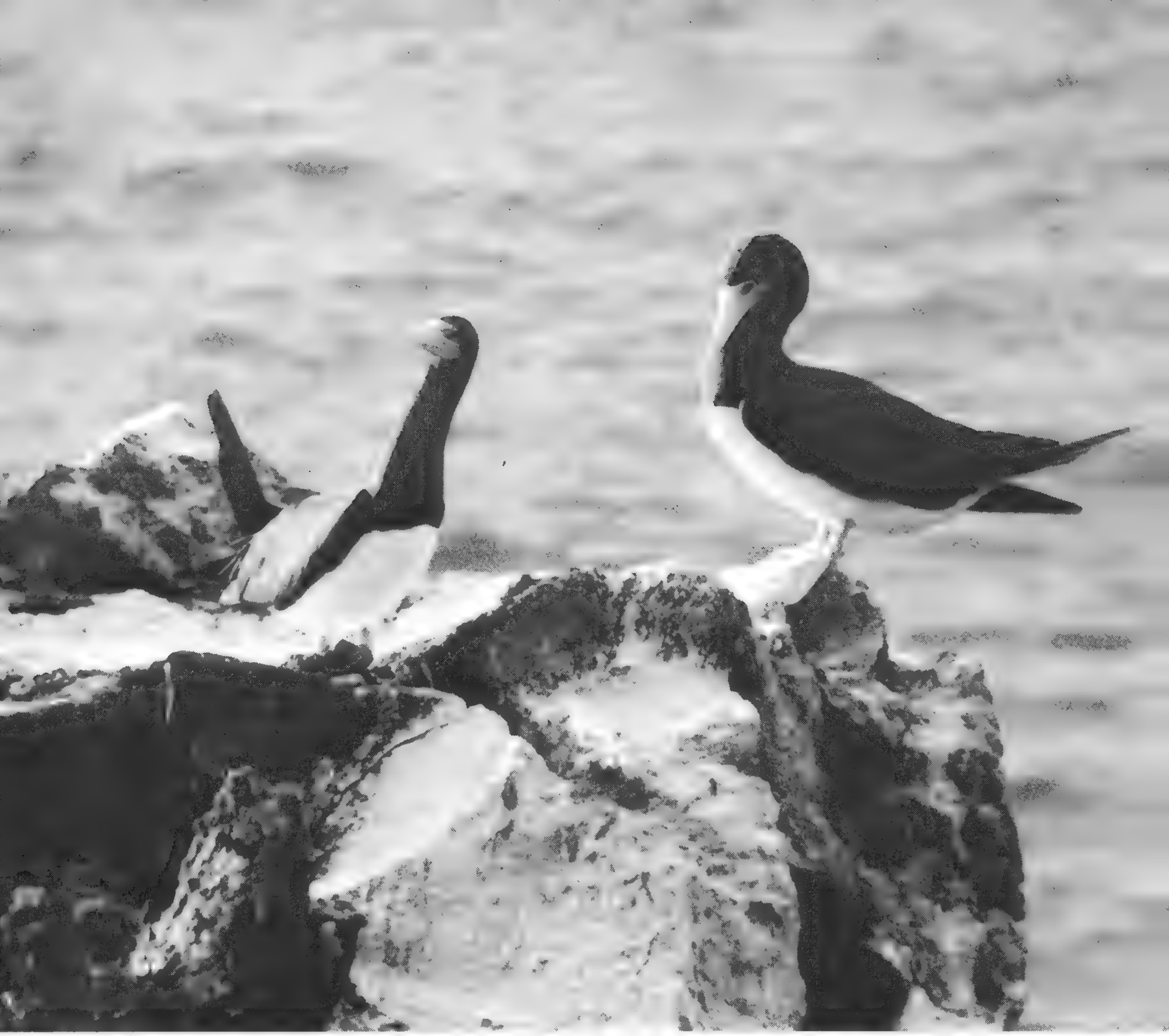


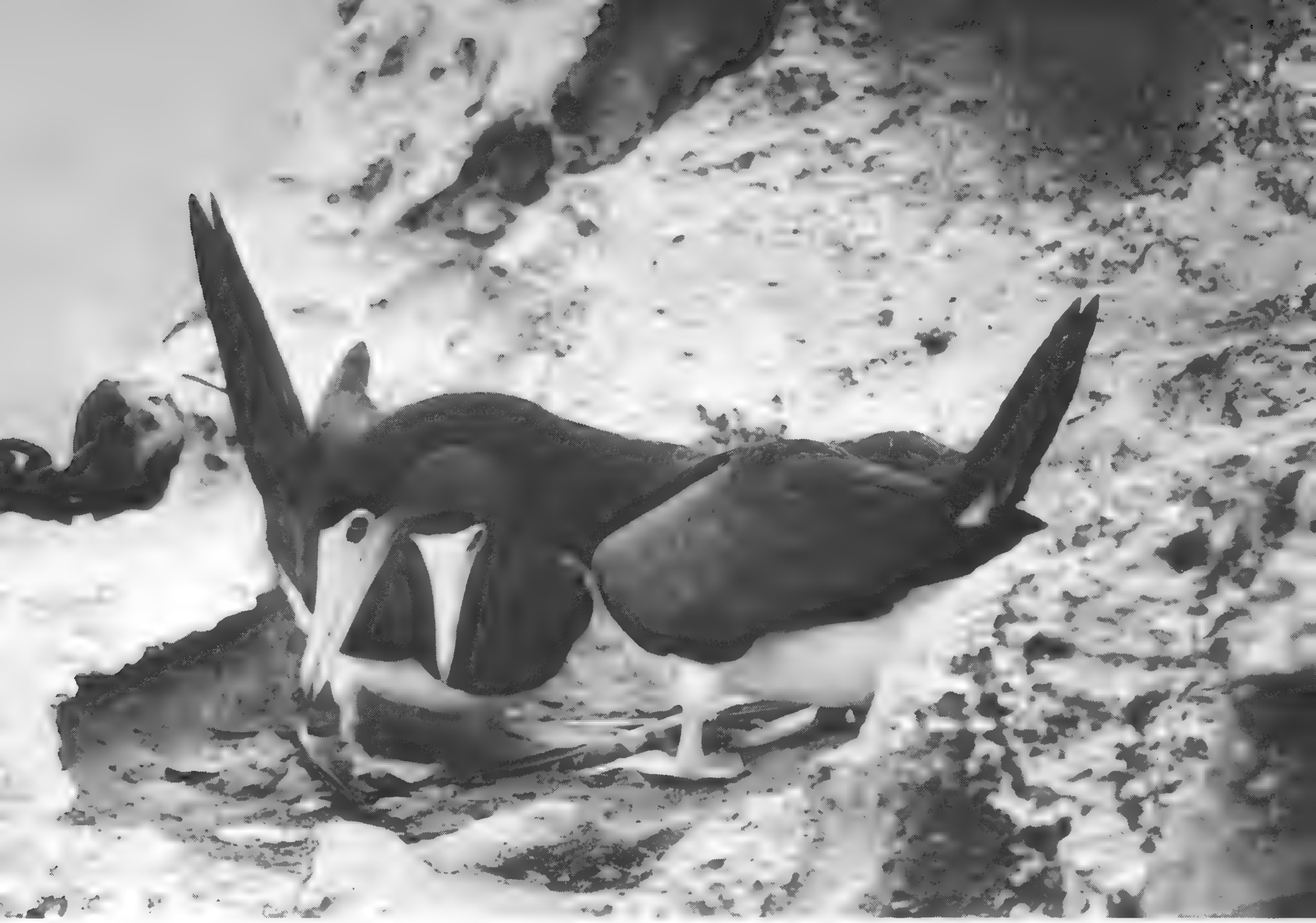
Figure 17. Male and female Brown Booby in an agonistic, pair-formation encounter. The male (left) is starting to Parade while Facing-away; the female is Bill-tucking. Photograph by the author, Stack 1, 10 December 1962.

averting activities clearly function to reduce hostile responses in the partner by removing the frontal, potentially antagonistic, orientation of the bill, which is likely to evoke hostility, especially from the bird occupying the nest-site.

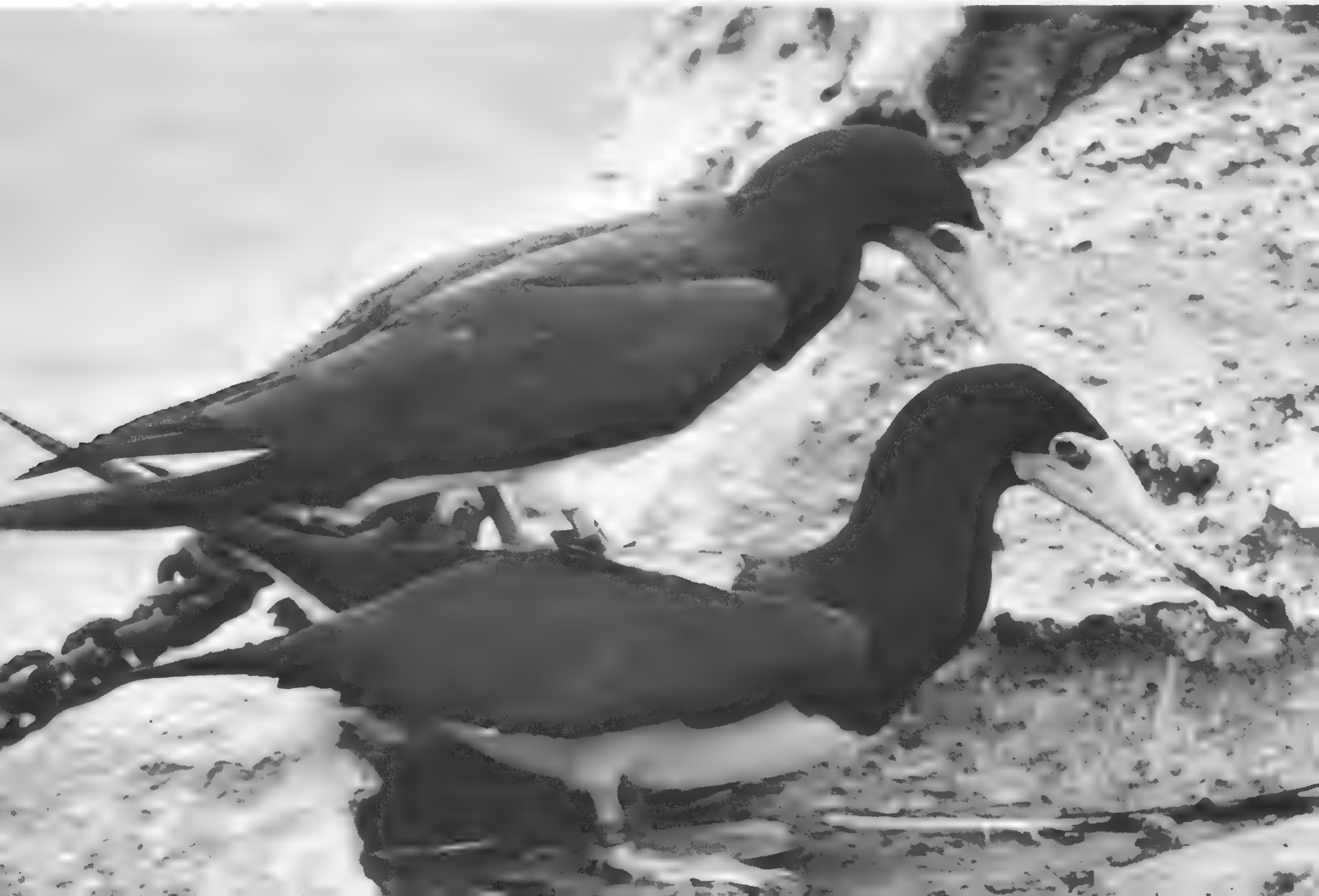
As well as appearing in sequences of behavior initiated by Sparring, Bill-averting is also shown by Bowing birds which often lower the bill to the side away from the partner, thus concealing it to a greater or lesser extent. After Bill-pointing, especially in the Greeting-ceremony, male and female are very likely to Bow-away from one another, more often simultaneously or successively, but sometimes unilaterally.

Nest-activity

Billing-and-bowing is a sequence which often initiates Nest-activity, particularly in the immediate pre-egg period. This fluid behavior pattern involves mutual and unilateral mandibulation, placing, fixing, raising, showing, and presenting of nest-material as the two birds stand together in the nest-hollow or Parade round one another in it, sometimes Neck-crossing (Figure 18) by reaching with the bill over the neck of the partner so as to peck at material beyond. Both birds utter their respective Nest-calls which are



Figures 18–22. Mating-ceremony of the Brown Booby during Nest-activity. Photographs by D. F. Dorward, Boatswainbird Island. Figure 18 (*above*): The female Neck-crosses as she reaches for a feather on the other side of the male. Figure 19 (*below*): She holds and Quiver-nibbles the feather while the male stands on her back and Bill-dips to the side of her head in the first stages of copulation. Figure 20 (*opposite, upper*): The male positions himself in the later stages of copulation, with his weight now on the flat of his tarsi and his tail to one side of the female prior to Tail-brushing. The female is still holding the feather. Figure 21 (*opposite, middle*): The female assuming the more aggressive role in a bout of Pushing. Figure 22 (*opposite, lower*): The male and female now Bill, but the male is still somewhat "apprehensive."



distinctive variants of the usual sex-specific ones. This is particularly true in the female which gives a series of monotonous, spaced grunts so characteristic of this situation. During Nest-activity, the birds may also Bill and Spar. Periodically, the male may Parade away and fly out to look for more nest material, or both sexes may ceremonially change places, each in turn occupying the center of the nest (Symbolic-relief). While Nest-activity is often "self-exhausting," it usually develops, during the immediate pre-egg period, into the Mating-ceremony. The male often initiates this behavior by repeatedly bringing nesting material, surrendering the center of the nest to the female, and "indicating" a particular piece of material to her while Neck-crossing, as well as Pawing at her side in incipient Mounting. However, he rarely Mounts unless the female herself Solicits. This she does in a highly specific manner by: (1) ceasing to give her characteristic Nest-calls; (2) remaining stationary in the center of the nest-hollow; and (3) Quiver-nibbling (Figure 19) a piece of nest-material in her bill close to the bottom of the nest, with her neck arched and head in a frontal downward position.

When performing her very distinctive Quiver-nibbling, the female holds a single item of material and nibbles it in a "pre-occupied" manner in the tip of her bill, while simultaneously quivering or trembling her head and bill from side to side, all the movements having a tiny amplitude while the head itself stays in its original downward position. During a full Mating-ceremony, the female continues to hold and mandibulate her bit of material while the male is mounted. When he dismounts, she usually deposits the material in the nest. Alternatively, she sometimes assumes the Copulatory-long-forward posture, with the head and neck fully extended near the ground and obliquely in line with her body. After Mounting, the male initially stands on the female's shoulders and then positions himself for copulation, at first rhythmically dipping his bill towards the back of her head, and either points alternately on each side of her neck, passes his closed mandibles through the feathers of her nape, nibbles her crown feathers or facial skin, or occasionally reaches for the material she is holding. Thus, while the male may modify his behavior at this stage, he never seizes the female's head and "subdues" her as does the male gannet (*Morus* spp.).

In the second stage of positioning, the male works himself backwards until his weight is transferred from his toes to the flat of his tarsi, then lowers his tail under the female's own raised tail and, with a side-to-side Tail-brushing movement (Figure 20), aligns his cloaca and Thrusts. In many instances, ejaculation does not follow, in which case the Mating-ceremony is mainly stimulatory ("self-exhausting"). In many other instances, of course, especially prior to egg-laying, insemination does occur. After Thrusting and its recovery movement, Rearing, in which he stands up on his toes once more, the male dismounts. He may then join with the female in arranging nesting material. More commonly, however, he first Parades away from her for a short distance, often with his bill averted, especially if there has been a bout of postcopulatory Sparring (Figure 21) and Billing (Figure 22).

The female's mood varies during the Mating-ceremony and the preceding Nest-activity. If she is ready for copulation, she is often extremely passive—an unusual characteristic of the usually aggressive female. Conversely, if she is not ready, she can be exceedingly aggressive toward the male. She may Spar forcibly with him if he shows any sign of Mounting and, if he does Mount, move away from under him or turn her head round and drive him from her back with vigorous movements of the bill. Not infrequently, even if she has Solicited, the female may terminate the Mating-ceremony at any stage in the same manner. The male then Parades away with the Bill-averted. Finally, the female Brown Booby may even exercise the avian equivalent of birth control. When receptive, her cloaca expands and contracts in spasms thus, most probably, facilitating insemination when the male ejaculates. However, on some occasions, I noted that this activity was absent and, instead, the female defecated copiously as the male Thrust.

Conclusion

It is evident that much of the social interaction between male and female Brown Booby consists of sustained "bonding" behavior, not directly connected with copulation but essentially appeasing, thus enabling the birds to remain together in the nesting territory without serious fighting. This "fringe" system ensures that the center "core" of strictly sexual behavior—the stimulating Nest-activity and Mating-ceremony — can take place without serious inhibition and lead to copulation when conditions for breeding are favorable.

Summary

For two years, 1962–1964, and three weeks in April, 1966, I studied two colonies of the Brown Booby (*Sula leucogaster*), one on each of two inshore stacks off the northwest coast of Ascension Island in the mid-central Atlantic Ocean.

In the first half of this paper I have discussed the coloration of both the adults and young, the feeding behavior both around Ascension and in the open sea, and the food supply that fluctuates irregularly throughout the year.

The average mortality is low for adult Brown Boobies and high for their eggs and chicks, the loss of eggs and chicks being mainly due to the instability of the food supply. I studied the breeding cycle and outlined the system of adaptations that have developed for breeding in a seasonless environment with an unpredictable food supply.

The last half of the paper deals with some of the determinates in the social behavior of the Brown Booby, including the behavior patterns that are ritualized and those that are more fluid.

Brown Boobies occupy a permanent nest-site and thus show a strong, aggressive behavior in protecting it at all times. Their trend towards "spaced" nesting and "steep" nesting results in a freedom of movement and an emphasis on aerial activity in the birds' antagonistic repertory. Landing calls are well developed; post-landing displays are undifferentiated. The female, larger and more aggressive, plays an important role in site defense and "dominates" in sexual activities.

I have discussed the behavior and displays of the booby pair on or near the nest-site when the birds are: (1) out-of-contact-range, (2) meeting after a separation, (3) at sustained close proximity, and (4) when they are moving apart. A male-specific behavior, Saluting, has been considered in detail.

The actions leading up to and during copulation are described. The behavior of the Brown Booby in the nest-territory has evolved as a "bonding" behavior, so arranged that Nest-activity and Mating-ceremony can quickly lead to copulation and breeding whenever food conditions are favorable.

Acknowledgments

My field work at Ascension in 1962–1964 was carried out privately with the sole help of my wife. Since then, however, I have received assistance in various forms from several sources which will be fully acknowledged elsewhere. In particular, from 1964–1966, I was supported financially by the Leverhulme Trust and given facilities for work at the Department of Psychology, University of Bristol, England, through the good offices of the late Prof. K. R. L. Hall and Dr. J. H. Crook. The work of Dr. Crook on the adaptive significance of avian social systems (e.g., Crook, 1965) has been of great heuristic value to my own studies. The 1966 visit to Ascension was financed mainly by the Leverhulme Trust and the British Ornithologists' Union, and accommodation and traveling facilities on the Island were provided by Pan American Airways. For the present paper, Robert Gillmor most kindly prepared all line drawings, while Drs. J. M. Cullen and D. F. Dorward (members of the BOU Centenary Expedition to Ascension) provided photographs. Dr. Dorward supplied the banding schedules from the BOU Expedition.

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MIGRATORY FLIGHTS OF *HYLOCICHLA* THRUSHES IN SPRING: A RADIOTELEMETRY STUDY

W. W. Cochran, G. G. Montgomery, and R. R. Graber

The tagging of animals with miniature radio transmitters has enabled biologists to study aspects of animal behavior that were impossible to even observe before about 1960. Since 1960, Lord *et al.* (1962), Singer (1963), Eliassen (1963), Southern (1964), and Michener and Walcott (1966) have all reported the use of radiotelemetry for following or obtaining physiological information on birds in flight.

The transmitters, used in the above studies, varied in weight from 16 to about 75 grams and were, therefore, too heavy for use on *Hylocichla* thrushes weighing 30 to 40 grams. In January 1965, we designed a 2.5-gram transmitter that was suitable for use on thrushes. During May of 1965 and April and May of 1966, using transmitters of this design and appropriate receiving equipment, we followed a total of 21 thrushes of three species for all or part of their night migratory flights. The species—Veery (*Hylocichla fuscescens*), Swainson's Thrush (*H. ustulata*), and Gray-cheeked Thrush (*H. minima*)—winter in South or Central America and are present in Illinois in spring only as transients on their way to breeding areas, essentially in boreal North America.

Methods

The Transmitter

The transmitter (see Figure 1 and Cochran, 1965) emits a pulsating signal which is heard with a receiver as an interrupted tone (*beep-beep-beep*). The weights of transmitters used in the study varied from about 2.3 to 2.8 grams, depending upon the quantity of cement necessary to strengthen and encapsulate the transmitter components. Newly constructed transmitters with a minimum of cement weighed less than 2.5 grams. Reused transmitters, to which we added cement every time we replaced the battery and antennas, increased the weight to as much as 2.8 grams.

Attaching the Transmitters to Thrushes

A radio-tagged thrush is shown in Figure 2. We attached transmitters to thrushes with Eastman 910 adhesive (Baldwin-Lima-Hamilton Corporation, Waltham, Massachusetts). First, we removed 15 to 20 feathers from the dorsal feather tract between the wings and applied a thin film of adhesive both to the bared strip of skin and to the lower surface of the transmitter. After the adhesive had become tacky from exposure to air for 10 to 15 seconds, we pressed the transmitter to the bird's back and held it firmly in place for about two minutes. We then released the bird. Although we tried to be consistent in our attachment technique, we had highly variable results. At least one transmitter remained on for five days, whereas several came off within a few hours after release. We suspect that the performance of the adhesive varied between individual bottles of adhesive and also with humidity. We are certain that the use of too much adhesive caused attachment failures and that waiting the right length of time for the adhesive to become tacky improved the bond. However, we found no practical way to accurately measure or control these variables under field conditions.

Attachment failures also resulted when the transmitter antennas caught in brush, particularly when the antennas were longer than about 12 inches. We discovered that the sacrifice in range of reception due to using a 12-inch antenna was acceptable (19 inches is optimum for range).

Influence of the Transmitter on Thrush Behavior

It is axiomatic that attachment of a transmitter to a bird affects its behavior. The addition of a 2.5-gram transmitter increases the weight of a 32-gram thrush by eight per cent, and the transmitter and its antenna, by reducing the streamlining of a bird to some degree, increase the drag during flight. Both factors increase the energy requirement for flight. That we observed radio-tagged thrushes migrating at air speeds up to 40 miles per hour (mph) and for as long as eight hours is some indication that the increase in energy requirement was not enough to affect the birds appreciably.

Graber and Wunderle (1966), in a discussion of the behavior of small radio-tagged birds, including a 30-gram House Sparrow (*Passer domesticus*) carrying a 4.7-gram transmitter, state that this sparrow "could fly well, climb, and maneuver sharply without obvious difficulty." Michener and Walcott (1966) could detect no noticeable difference in the flight performances of Homing Pigeons (*Columba livia*) carrying transmitters weighing about 15 per cent of pigeon body weight. Both the House Sparrow and the Homing Pigeon had radio transmitters fastened on the back, between the wings.

Following Thrushes

In the spring of 1965 we used a radio-equipped airplane (Figure 3) to follow migrating thrushes. The operational procedures involved in following a bird's flight by airplane are given by Graber (1965) in his description of the thrush flight referred to in this paper as Flight 7.

In the spring of 1966 we used receiving equipment installed in a carry-all truck (Figure 4). We determined the flight paths by periodically driving to locations where the bird was expected to cross a road (Figure 5). As we neared the estimated cross-over point, we drove at speeds which tended to maintain a constant bearing from the truck to the bird, alternately increasing speed when the bearing shifted toward the front of the truck and decreasing speed when the bearing shifted toward the rear. A rapid decrease in signal strength, as the bird flew through an overhead receiving antenna null, followed by a signal increase and shift in bearing to the opposite side of the truck indicated that the bird had passed overhead. The time and location of the cross-overs, when plotted on a road map, provided a plot of the bird's course and speed as the flight progressed, and enabled us to select roads and truck speeds to take us to the next convenient cross-over location. We estimate the accuracy of the bird locations, obtained in this way, to be better than plus or minus 0.25 mile.

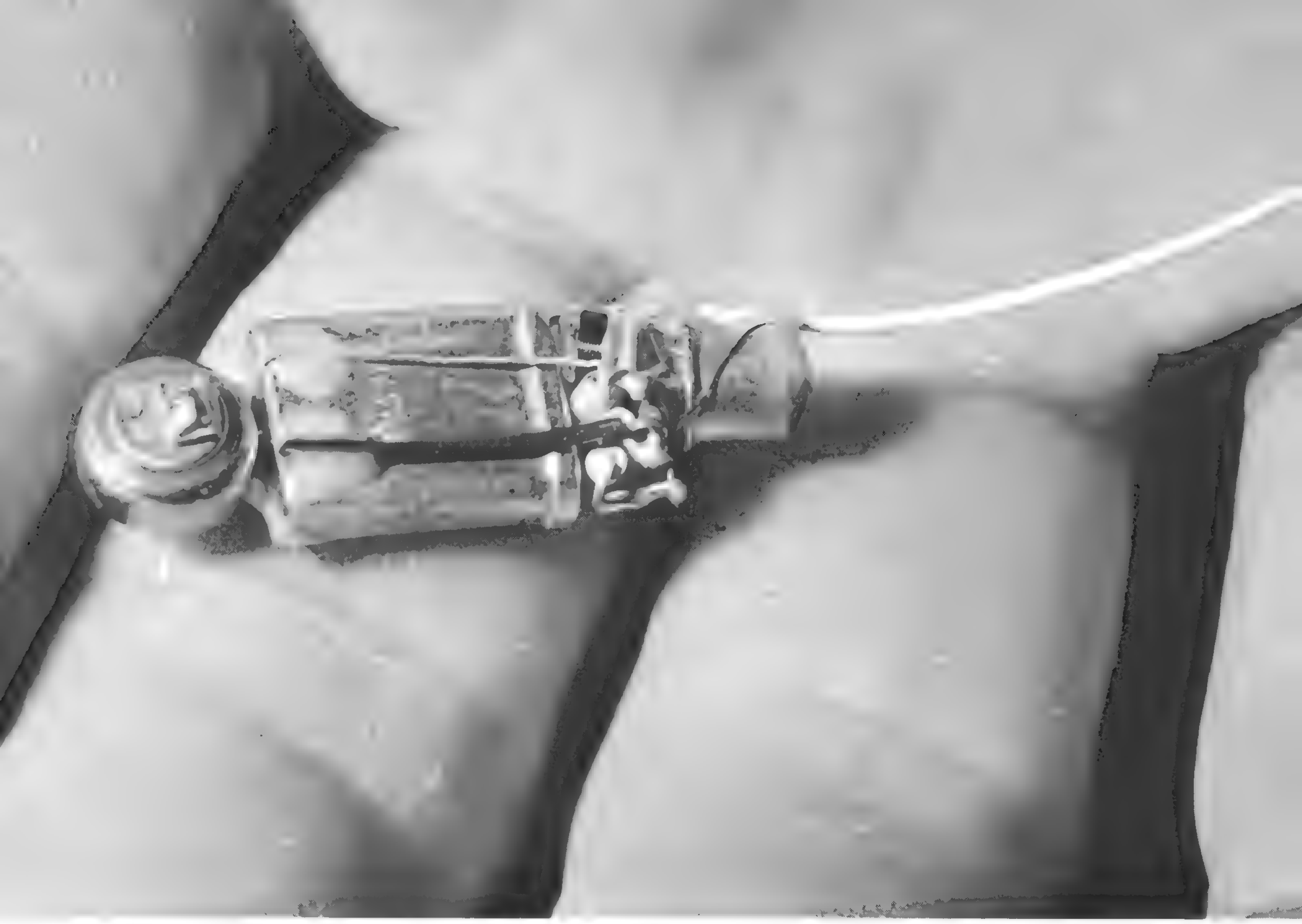
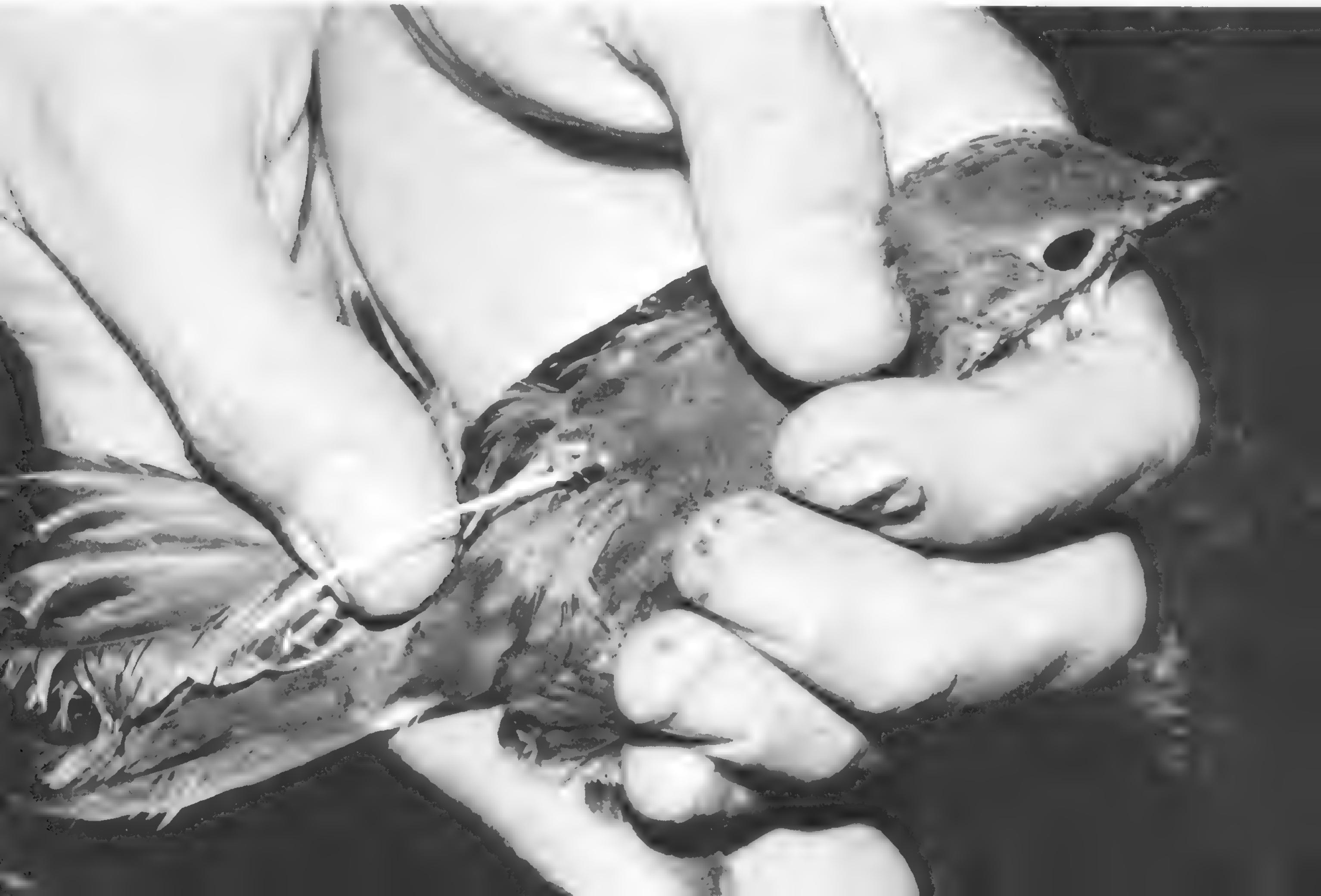


Figure 1 (*above*). This view of the transmitter shows (left to right) the battery, crystal, transistor, and part of the antenna. Coils, resistors, and capacitors are compactly arranged between the crystal and transistor. When the area between the crystal and antenna becomes wet the transmitter pulse rate increases. Dabs of cement bond the antenna, battery, and battery-leads to the transmitter. Photograph by W. D. Zehr.

Figure 2 (*below*). A radio-tagged thrush. Note that feathers almost completely cover the transmitter. The first 2 inches of the 12-inch music wire antenna are covered with a thin plastic sleeve. Photograph by W. D. Zehr.



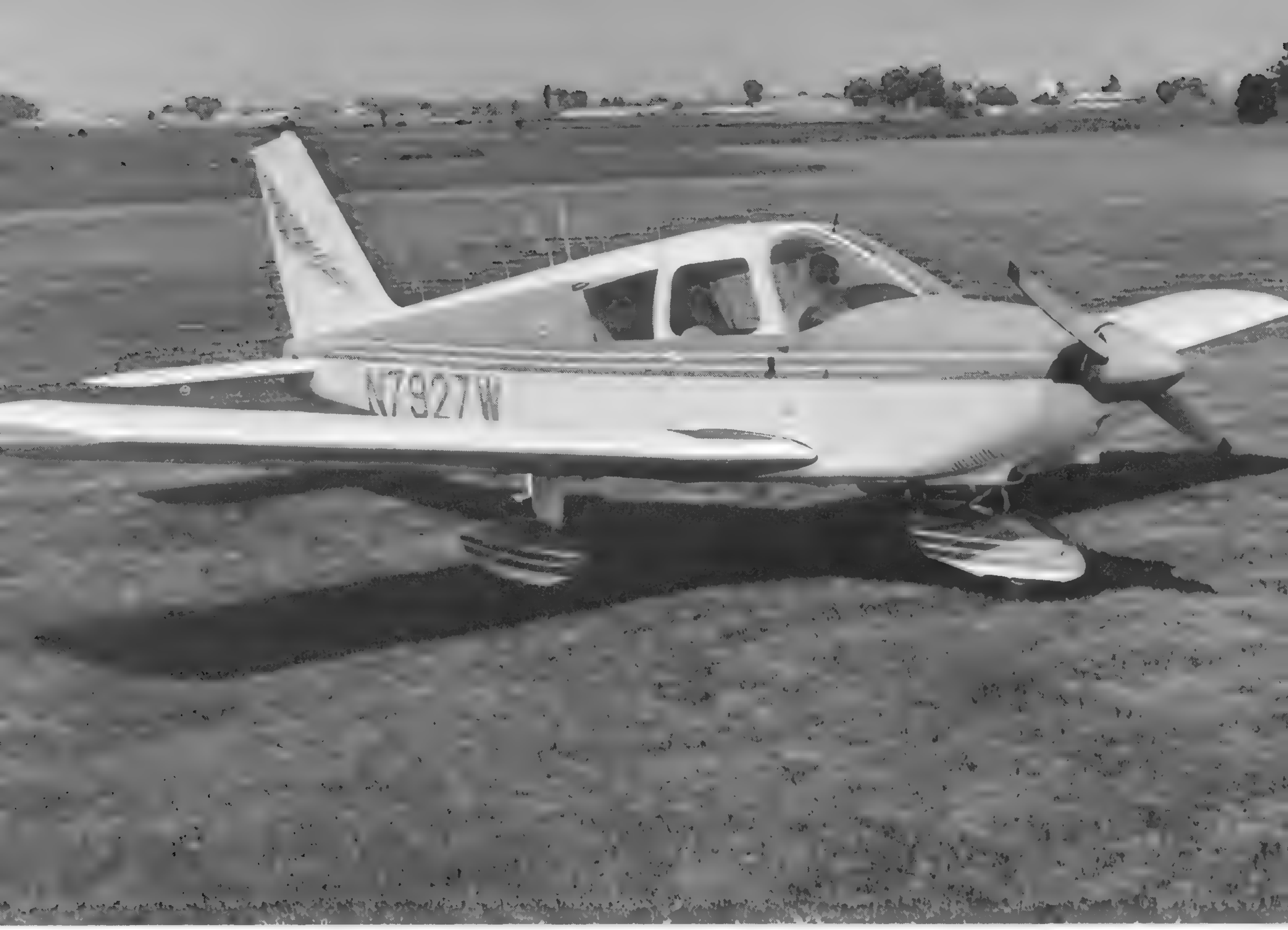
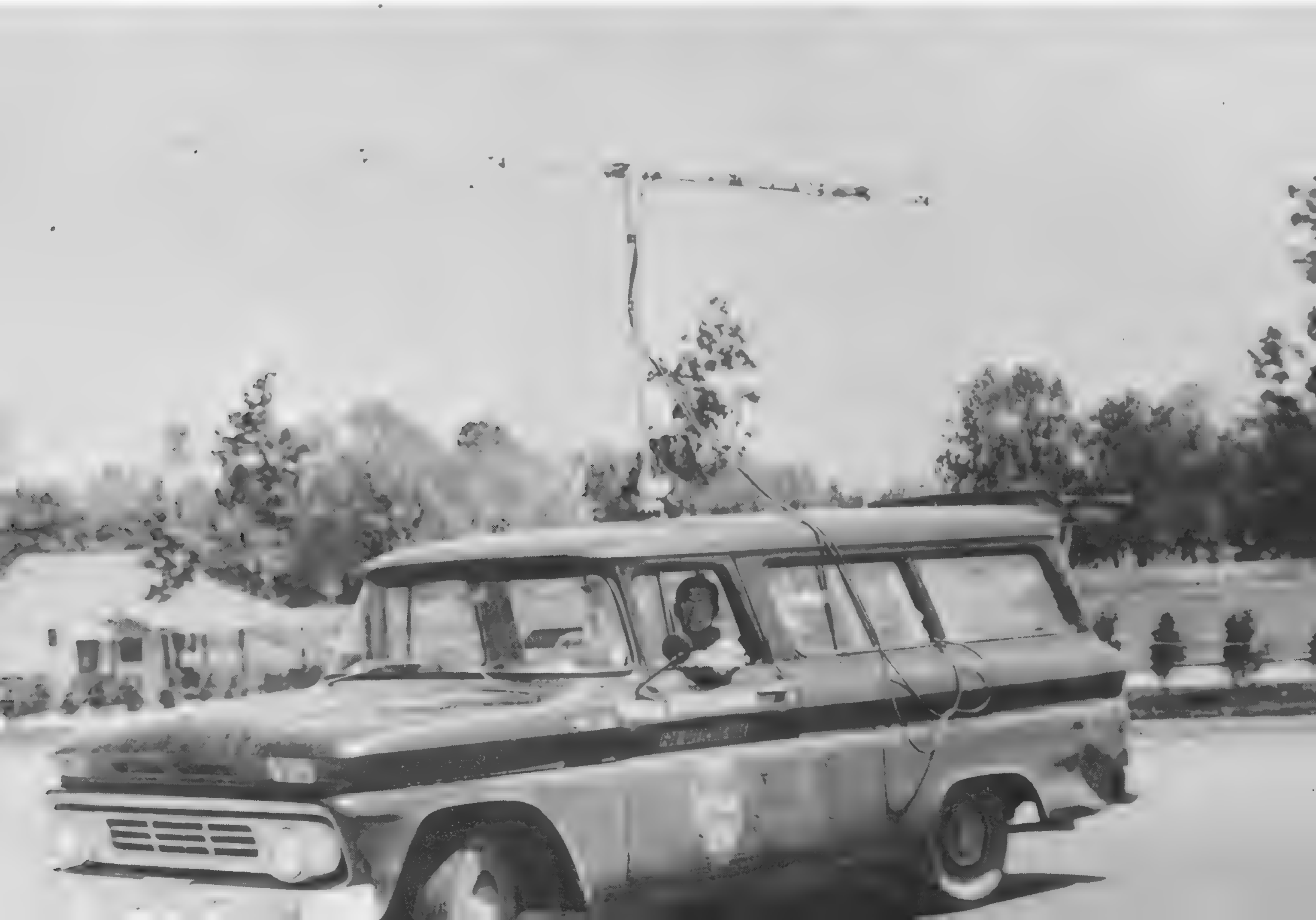


Figure 3 (*above*). The Piper Cherokee 180 used for observing Flights 1 through 7 (excepting 5b). The six shorter antennas arranged lengthwise along the plane comprise the quarter-wave vertical yagi used for homing on the birds. The three longer antennas located about midway along this array were for communications. Photograph by W. D. Zehr.

Figure 4 (*below*). Carry-all truck equipped for following radio-tagged migrants. The 14-foot-long directional antenna was rotated from inside by an equipment operator (not shown) in a seat behind the driver.



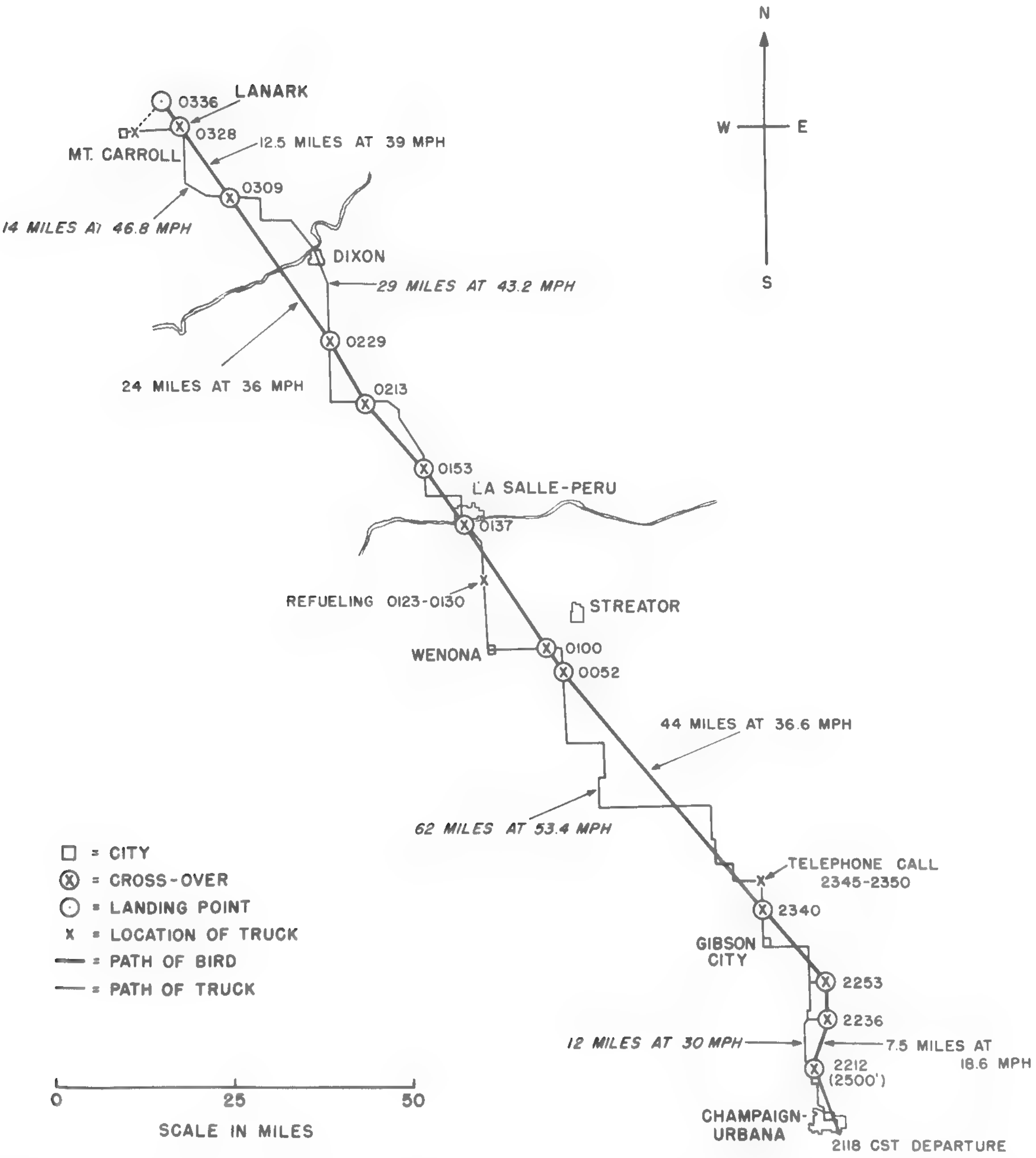

N
W
E
S
0336
LANARK
0328
MT. CARROLL
12.5 MILES AT 39 MPH
0309
14 MILES AT 46.8 MPH
DIXON
29 MILES AT 43.2 MPH
0229
24 MILES AT 36 MPH
0213
0153
LA SALLE-PERU
0137
REFUELING 0123-0130
STREATOR
WENONA
0100
0052
44 MILES AT 36.6 MPH
62 MILES AT 53.4 MPH
TELEPHONE CALL 2345-2350
2340
GIBSON CITY
2253
2236
12 MILES AT 30 MPH
7.5 MILES AT 18.6 MPH
2212 (2500')
CHAMPAIGN-URBANA
2118 CST DEPARTURE
□ = CITY
⊗ = CROSS-OVER
⊙ = LANDING POINT
x = LOCATION OF TRUCK
= PATH OF BIRD
= PATH OF TRUCK
0
25
50
SCALE IN MILES

Figure 5. Paths taken by a Veery (Flight 11) and the truck, illustrating the technique used to reach cross-over points. Note that the truck speed was greater than the ground speed of the thrush during all parts of the flight, and particularly from 2350 CST to 0052 CST after we stopped to telephone.

The range of reception from the truck varied from a few miles to a bird flying at an altitude of a few hundred feet to over 12 miles to birds at 3,000 to 5,000 feet. Crude altitude estimates were made by determining the maximum range of reception at times when roads forced us to deviate a considerable distance from the bird's flight path.

Calculation of Flight Headings and Air Speeds

We calculated bird headings and air speeds by constructing vector triangles using bird ground speeds and directions and wind speeds and directions (Allen, 1939). Track information was usually accurate to one or two miles per hour and two or three degrees. Wind data were subject to large errors. Birds seldom flew near US Weather Bureau winds-aloft measuring stations; therefore, we had to interpolate between these stations. Also, we often needed wind data for periods two or three hours different from the times for which wind measurements were available; this required interpolation in time. If the wind change was considerable between stations or between observation times, or both, interpolation may often have resulted in wind speed errors as high as 40 per cent and direction errors as high as 30 degrees. Another source of error was in our estimates of altitudes of the birds; these were probably within 30 per cent of the true altitudes. When winds varied significantly with altitude, as they often did, this percentage error resulted in additional errors in air speed and heading calculations. Estimates of errors were made by constructing wind triangles for all the possible data within the limits of estimated error for each parameter, and taking the most deviant values of heading and air speed so obtained as the probable range of error. Table 1 gives track direction, air speed, heading data, and the estimated ranges of error of each. These data are for the portions of flights requiring a minimum interpolation of wind data.

TABLE 1

Summary of Data on Migratory Flights of *Hylocichla* Thrushes

Flight (bird) number	*Date of departure*	*Ground speed (mph)*	*Air speed (mph)*	*Track direction (degrees)*	*Heading (degrees)*
SWAINSON'S THRUSH					
3	13 May 1965	41 ± 2	43 ± 5	305 ± 2	298 ± 17
5a	18 May	21 ± 2*	29 ± 3*	266 ± 2*	300 ± 12*
5b	19 May	24 ± 2	20 ± 4	293 ± 5	302 ± 8
6†	21 May	29 ± 3	29 ± 5	353 ± 3	335 ± 10
9	29 April 1966	38 ± 1	34 ± 3	045 ± 1	065 ± 9
10	5 May	60 ± 2	30 ± 15	090 ± 3	060 ± 15
12	13 May	20 ± 1	15 ± 3	180 ± 4	180 ± 8
13	16 May	42 ± 1	30 ± 4	302 ± 2	295 ± 5
14	16 May	—	—	302 ± 5	—
15	17 May	46 ± 3	34 ± 7	000 ± 2	000 ± 5
17	19 May	30 ± 1	20 ± 3	080 ± 2	038 ± 12
20†	23 May	—	—	045 ± 15	—
GRAY-CHEEKED THRUSH					
2	8 May 1965	—	—	010 ± 5	010 ± 15
4†	17 May	38 ± 4	29 ± 12	010 ± 5	007 ± 10
7†	24 May	52 ± 2	25 ± 4	010 ± 2	355 ± 8
8	28 April 1966	43 ± 1	34 ± 3	230 ± 1	194 ± 5
16	18 May	—	—	045 ± 20	—
18†	20 May	37 ± 1	26 ± 4	255 ± 1	250 ± 5
19	21 May	38 ± 1	31 ± 3	325 ± 1	325 ± 10
21	27 May	26 ± 1	29 ± 2	035 ± 1	005 ± 7
VEERY					
1	7 May 1965	—	—	010 ± 5	010 ± 10
11	6 May 1966	32 ± 1	40 ± 3	327 ± 1	320 ± 5

*The average of several values representative of different portions of the flight.

†Immature.

Aging and Identifying Thrushes

We identified thrushes as immature if we noted the presence of spotted wing coverts. However, since the absence of these spots does not definitely indicate that an individual is adult (Payne, 1961), those individuals not noted as immature are considered to be of unknown age. A large percentage of these "unknowns" was probably adult (*ibid.*).

Because of the inherent difficulty in identifying individual thrushes to subspecies, and because we did not want to hold birds longer than necessary, we made no attempt to identify subspecies in the birds we radio-tagged. The following subspecies of *Hylocichla* have been recorded in Illinois: For the Veery, both *H. f. fuscescens* and *H. f. salisicola;* for the Swainson's Thrush, *H. u. almae* and *H. u. swainsoni;* and for the Gray-cheeked Thrush, *H. m. minimus.*

Results and Discussion

Activity of Grounded Migrants

Devlin (1954:93), Bagg (1957:325), and Vleugel (1960:14) report observing nocturnal migrants proceeding by day. None of the 33 thrushes observed during our study proceeded by day; all confined their daytime activity to 0.1- to 0.5-acre areas. Even the two birds that we followed to landing points in extensively wooded areas confined their diurnal activities to small areas. We conclude that, in spring and in the geographical area of the study, these three species of thrushes do not migrate during daylight.

Initiation of Flights

Departure times are shown in Figure 6. (Time is given as 0000 equals midnight.) Although departures occurred from 1945 Central Standard Time through 0144 CST, most occurred before 2100 CST. More irregularity in departure time occurred in 1966 than in 1965, which probably reflects the greater variability in the weather conditions under which we observed radio-tagged birds in 1966. In 1965 we intentionally tagged birds only on days judged ideal for migratory flight.

Departures could sometimes be stimulated artificially by disturbing the birds. Flights 13, 14, and 20 were initiated by walking under the low trees where these birds were roosting. In one case we had to shake the tree before the thrush flew. We might also consider Flight 12 as artificially stimulated because the bird took flight as a train passed within 15 feet of its location in low bushes. As shown in Figure 6, three of these artificially stimulated flights (12, 14, 20) were of relatively short duration. The fourth (13) may have continued after we lost the signal.

On two occasions we tried unsuccessfully to stimulate flight. Shaking trees in which the thrushes were roosting resulted only in flights to adjacent trees. In one case, Montgomery climbed into the tree and picked up the bird which made no attempt to escape.

Although the number of migrants flying as the result of disturbances is probably small compared to the numbers which fly as a result of other stimuli, disturbance may not be too uncommon in nature, and could account for some migrants observed flying under obviously unfavorable conditions.

We shall report data on the percentage of birds departing under various weather conditions in a subsequent paper. Briefly, we found temperature to be positively correlated with the percentage of radio-tagged birds departing.

Flights Under Clear or Partly Cloudy Skies

Flight paths are shown in Figure 7. Flights 3, 5a, 5b, 7, 11, 17, 19, and 21 are probably representative of spring migration of *Hylocichla* passing through Illinois. These flights were characteristically of considerable duration (3.5 to 8.5 hours), at altitudes of 3,000 to 5,000 feet, and with headings toward some part of the breeding area. A few of these flights differed from most others in some respect and are described below.

Flights 5a and 5b represent the same bird on two successive days. The bird departed shortly after 2000 CST with an average heading of 300 degrees. Its first flight, Flight 5a, ended when the bird landed in a pine plantation after about 8.5 hours of flight under clear skies but with adverse winds (northwesterly, 16 to 30 mph). The bird was active during that day. About 1600 CST the sky began to cloud up and by 1900 CST it was overcast. At 1952 CST the bird departed with a surface wind from the east at 8 mph. We followed the bird by truck until 2153 CST when the signal was lost because of receiver battery failure. At this time it was raining lightly but by 2300 CST the skies were clear. The heading (302 degrees), taken by the bird under overcast skies, was within two degrees of the average heading (300 degrees) taken on its previous night's flight under clear skies. We estimate the altitude of the bird to have been between 3,000 and 5,000 feet after it crossed the Mississippi River.

Flight 21 was the only flight we observed for which there is a strong indication that ground cues resulted in a major course change. The flight took place at about the time a weak east-west cold front was 25 to 50 miles south of Lake Michigan extending through Illinois and Indiana. We are certain that

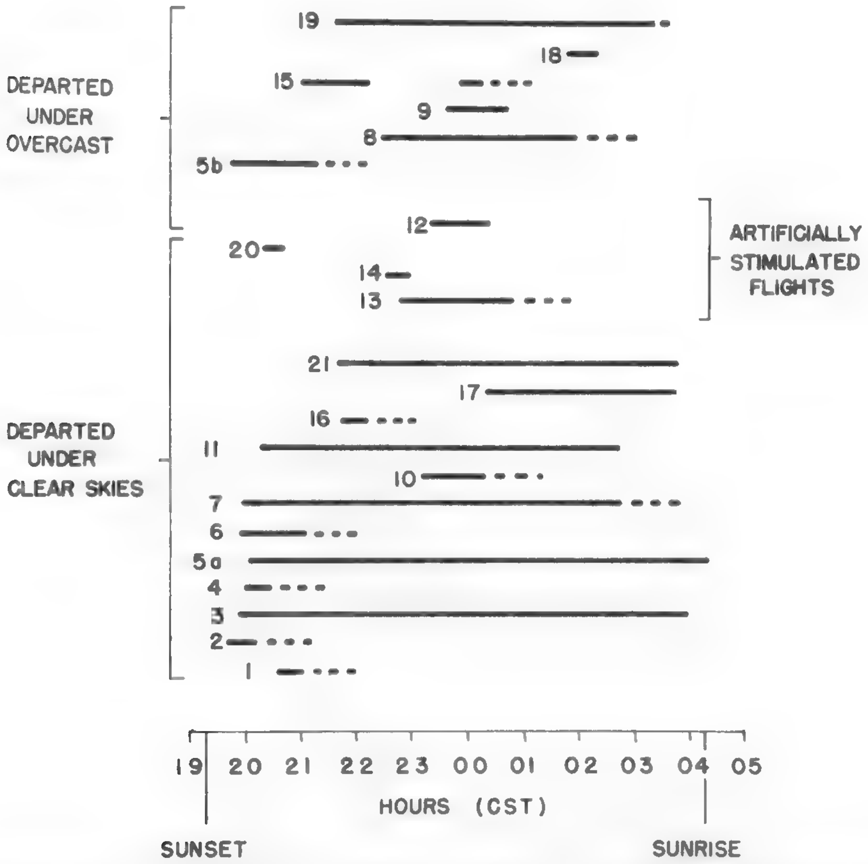


Figure 6. The timing and duration of flights by flight number. The dotted lines indicate that we lost radio-contact and therefore do not know how long the flight continued. Local twilight was a period of about 30 minutes after sunset and before sunrise.

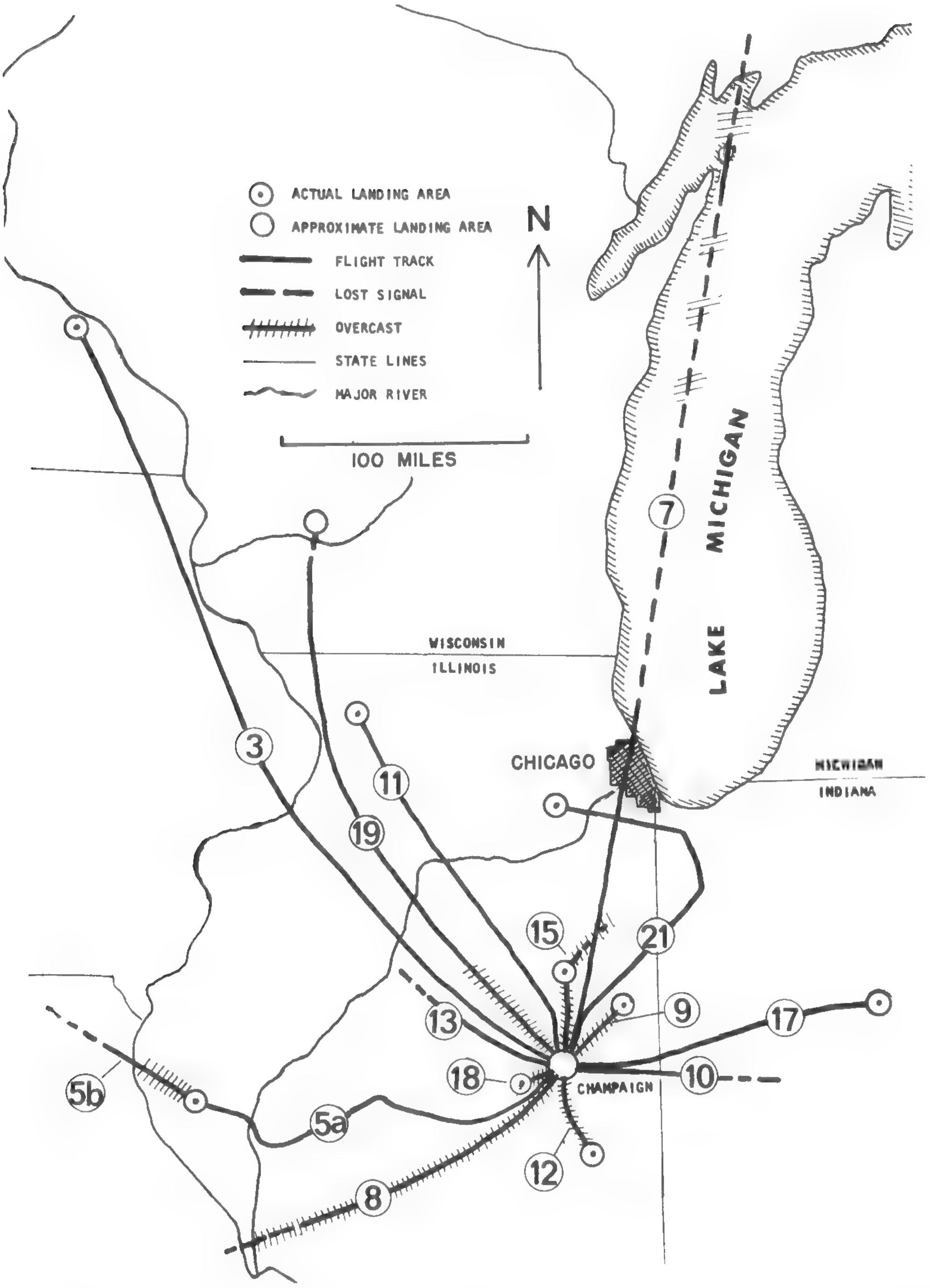

ACTUAL LANDING AREA
APPROXIMATE LANDING AREA
FLIGHT TRACK
LOST SIGNAL
OVERCAST
STATE LINES
MAJOR RIVER
N
100 MILES
WISCONSIN
ILLINOIS
CHICAGO
LAKE MICHIGAN
MICHIGAN
INDIANA
CHAMPAIGN
7
3
11
19
15
21
9
17
13
18
10
12
8
5a
5b

Figure 7. Tracks of birds followed for 20 or more miles. The irregularity in the path of 5a was due to variations in wind at the different altitudes flown by this bird during different portions of its flight. We could not estimate the altitudes of 3 and 19 accurately enough to determine if wind changes caused the curvature in their paths. Curvature in 21 is discussed in the text. Note that after breaking radio-contact while 7 was over the lake, we re-established contact for a brief period at the north end of the lake (Graber, 1965).

the bird's altitude was in excess of 4,000 feet, at least until it crossed into Indiana, because we received the signal from a distance of 40 miles with receiving equipment located near Champaign. Because winds above 3,000 feet were relatively constant from the west-northwest, we were able to make a fairly accurate wind analysis for this portion of the flight (Table 1). The first change in course occurred about 30 miles south of Lake Michigan (Figure 7). This change can be attributed to a change in the bird's heading if the bird remained at 4,000 feet, or to different winds if the bird's altitude was reduced to 2,000 feet with no change in heading. We were unable to make a sufficiently accurate estimate of the bird's altitude to choose between the two alternatives.

The second change in course occurred about 10 miles south of Lake Michigan, and cannot be accounted for by a change in wind direction at any altitude. Therefore, we are certain that the bird changed its heading. That this change occurred when the bird was within sight of the lake and lights in metropolitan Chicago, suggests that one or both of these may have influenced the bird. The flight ended in a direction (356 degrees) from Champaign which was close to the mean of the headings taken by four other radio-tagged Gray-cheeks (Figure 8) and was also close to the heading (005 degrees) taken during the first portion of Flight 21. This suggests that the change in course was a response to the lake or city as a cue which enabled the bird to correct for the wind drift that occurred during the first portion of its flight. However, we cannot rule out a response to the cold front or an arbitrary selection of a westward (instead of eastward) course to avoid the lake.

Flight 19 began under overcast sky, although during that day the sky was only partly cloudy. Surface wind at the time of departure was from the northeast at 4 mph. After maintaining a functional heading under the overcast for 25 to 80 miles (we did not note the exact time the overcast ended), the bird entered clear skies and continued its flight without a significant course change. The curvature in its flight path (Figure 7) occurred later, under clear skies.

Reversed Migration?

Flight 8 began at 2230 CST when the surface wind was calm. A cold front moved into Illinois during the day with temperatures in the 50's and a low that night of 50 ° F (the lowest for which we had a flight except for artificially stimulated Flight 12). The sky was partly cloudy during the day, becoming overcast toward evening and remaining so throughout the portion of the flight that we observed. We estimate that the bird flew at an altitude of 3,000 to 5,000 feet. Even at 5,000 feet, the bird was below the base of the clouds as measured at St. Louis at 2315 CST. During the last 30 miles that we were in radio-contact with the bird, we drove through scattered light rain but did not detect the effect of rain striking the transmitter. About 20 miles east of the Mississippi River we broke radio-contact in order to cross the river at Alton, Illinois. Our attempt to re-establish radio-contact on the west side of the river failed. This flight was similar to 5b and 19 in that these birds also departed under overcast and had partly cloudy skies during the daylight hours before departure. It differed from 5b and 19 in that the temperature was more than 10 degrees colder and the bird headed west-southwest. This suggests that this bird made a reverse migratory flight and was not disoriented by the overcast.

Flights in Bad Weather

These flights are interesting because they differed markedly from the majority and appeared to serve no useful purpose. Perhaps they should not be considered migratory. They may be generally described as down-wind flights at relatively low altitude with landings in open fields in total darkness (except for lightning flashes).

Flight 9 began under skies that had been overcast since early morning. After about one hour of flight at 500 to 1,000 feet, the bird landed in a field of winter wheat. After remaining near the landing point until dawn, the bird flew to a wooded area about 0.5 mile away. There was no rain during the flight but we noted distant lightning at about the time the bird landed. Surface wind was from the south at 8 mph at the time the bird departed.

The day of Flight 15 was overcast with temperatures in the high 60's and low 70's F. The sky was overcast and the surface wind from the south at 7 mph when the bird departed at 2104 CST. Shortly after departure, while the bird was flying north, moderate rain began and the fluctuating transmitter pulse

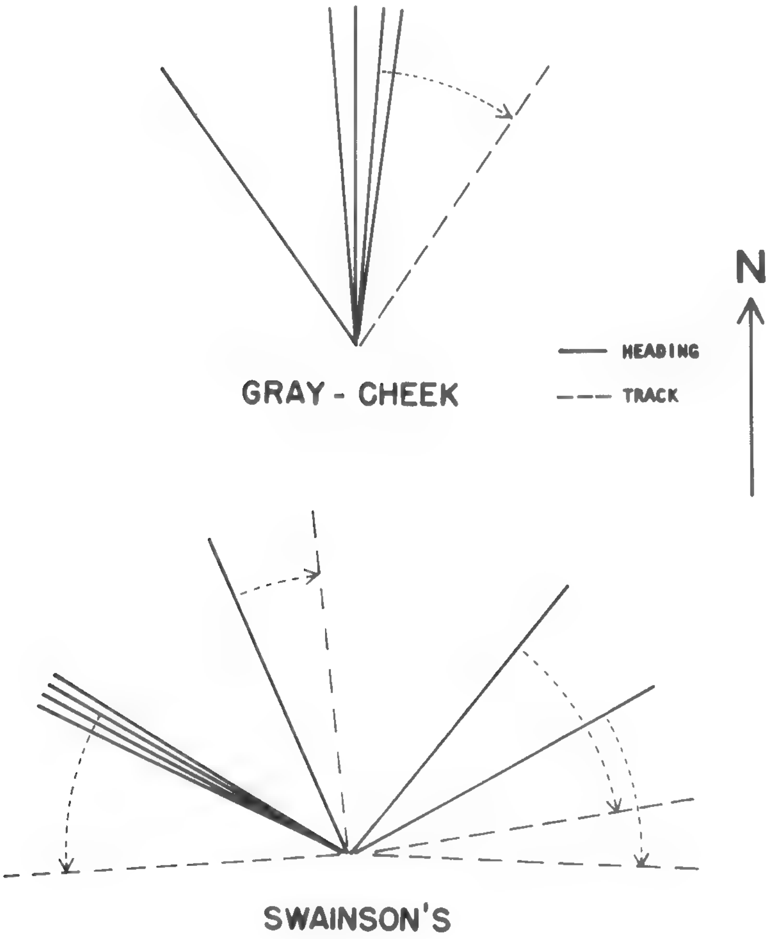


Figure 8. Solid lines are headings taken by five Gray-cheeked and seven Swainson's Thrushes under clear skies. Two of the headings shown are for birds that began their flights under overcast (5b and 19). Track direction (dashed lines) is shown only if the track differed from the heading by more than 10 degrees.

rate indicated that the bird was flying in this rain. After flying for 71 minutes, most of the time in the rain, the bird landed in an open pasture. After we reached the landing point we heard frequent and loud migrant calls overhead indicating that a considerable migration was taking place at low altitudes. About one hour after the thrush landed, a very hard rain and frequent lightning began. During the rain, and with a surface wind from the southwest at 14 mph, the bird departed and flew to the northeast. The transmitter pulse rate was continuously fast, indicating that the bird was flying in heavy rain, not merely encountering an occasional drop. About 10 minutes after departure we lost radio-contact because of a poor choice of roads and the limited range of reception due to lightning static. We estimate that both portions of the flight were at altitudes of less than 500 feet. One other radio-tagged bird did not fly that night.

Weather conditions the day of Flight 18 were very similar to those for Flight 15 with rain beginning at about 2200 CST. The bird departed at 0144 CST during a 20-minute lull in the rain and with a surface wind from the east at 8 mph. Hard rain began again about 10 minutes after the bird departed. Fluctuations in the transmitter pulse rate indicated that the bird was flying in the rain. After flying west-southwest for 31 minutes at an estimated altitude of 500 to 1,000 feet, the bird landed in an open field. Three other radio-tagged birds did not fly that night.

Conclusions

The study yielded a variety of data on spring *Hylocichla* migration from which we draw the following conclusions. The spring migration of these thrushes is entirely nocturnal, usually commencing 45 minutes to 2 hours after sunset and ending at dawn. On long flights the birds fly at altitudes of 2,000 to 6,000 feet. At least some individuals are capable of migrating on two successive nights. Air speed is usually less than ground speed, which suggests that these migrants are often aided by the wind. There is considerable variation, but most flights are at air speeds between 25 and 35 mph. The variability in headings is also quite large but Gray-cheeked Thrushes seem to head more directly north and Swainson's Thrushes northwest. The data suggest that these migrants have the capability of selecting a functional heading at departure under overcast, but to do so, probably require clear or partly cloudy skies during the day or evening before departure. Straight flights are maintained for a hundred or more miles under overcast. Excepting perhaps large topographical features such as Lake Michigan, ground cues are not used as route check-points. Flights of less than an hour's duration sometimes occur during or before thunderstorm activity. These flights are down-wind at low altitudes. The birds are capable of flying in heavy rain for at least one-half hour and voluntarily do so occasionally. When landing in darkness these migrants do not select their typical diurnal habitat but, instead, wait until dawn to find such habitat.

Because of the relatively small number of birds observed, and because the accuracies of most of the data are not sufficient to yield meaningful analyses of the effect of wind, we make no further attempt to extrapolate or interpret the data presented. One ornithologist, upon seeing our data—and observing that it was contradictory to some of his observations—suggested that the radio fastened to the birds was responsible for some of the behavior we observed. This point is well taken, for the near impossibility of providing controls dictates that studies using radio-tags are studies, not of birds, but of radio-tagged birds.

Acknowledgments

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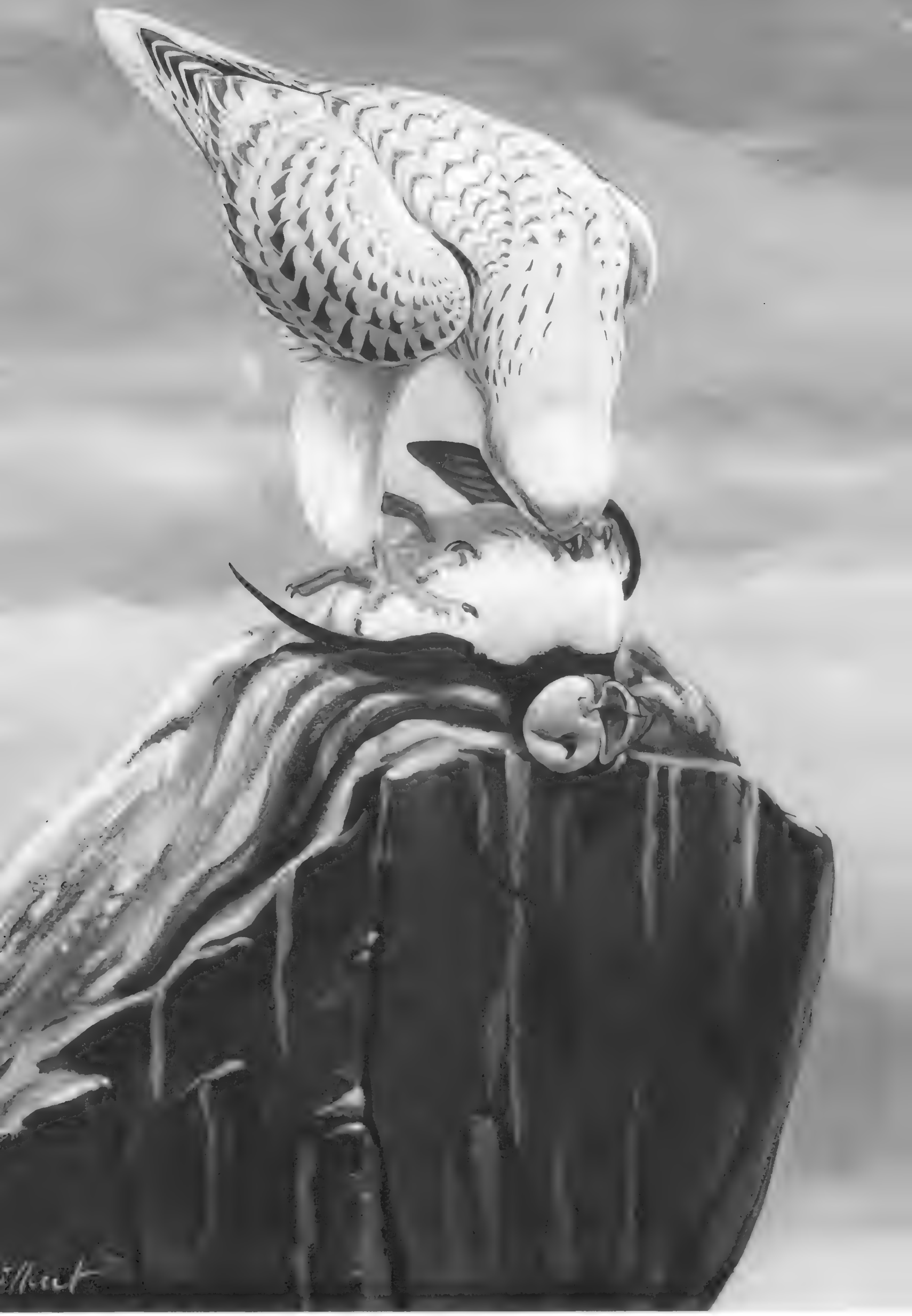

Gyrfalcon, *Falco rusticolus,* with Common Puffin, *Fratercula arctica*. Painting by Al Gilbert.

EGG-CARRYING BY THE PILEATED WOODPECKER[1]

Frederick Kent Truslow

Photographs by the author

In April 1966, a pair of Pileated Woodpeckers (*Dryocopus pileatus*) began carving what we all hoped would be a nest-hole in a new utility pole about 20 feet from the fire-equipment building in the headquarters utility section of Everglades National Park in Florida. After working on the pole for several days, the woodpeckers abandoned it and moved to a pine where they excavated a nest-hole in the trunk about 17 feet from the ground. Although the pine tree was dead with most of its branches missing and its top broken off about 32 feet above the ground, it was not rotten, and the birds worked hard chipping out the hole and excavating the interior. At this time they were noisy and relatively tame, paying no noticeable attention to me or to any other observers.

After the female laid her eggs and they settled down to the period of incubation, they became quiet and rather shy. They changed places on the nest very quickly and when the incubating bird peered out the hole to look about I could see only the head—up to the eyes.

On 6 April, I began watching this pair from a blind atop a 12-foot tower about 17 feet from the nest-tree. Concealed in this blind with my cameras, tripod, and photographic gadgets, I settled down to a period of waiting—photographing the nest exchanges, which occurred on the average of every two hours, yet might be as close as eight minutes, and observing the birds' general behavior.

The day of 16 April was exactly like the previous ten had been—very quiet with no noticeable air motion. Edward Carlson, a subdistrict ranger in the park, helped me into my blind, as he had on previous occasions, and acted as my "go-away"—i.e., the second person who walks away from the blind so as to fool the birds which cannot count. At 2:05 PM, I zipped up the entrance to my blind and adjusted my camera, sticking the 400 mm lens through the lens port and aiming it at the nest-hole. Then I waited for action.

At 2:45 there was a nest exchange; the male departed and the female took over. I photographed the change and relaxed. Nothing would happen for a few minutes at least.

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[1] An abbreviated version of this paper by the same author appeared under the title "When Disaster Struck a Woodpecker's Home" in the *National Geographic Magazine* (130:882-884, December, 1966).

Suddenly there was a shattering noise—a tearing, lengthening crash. I looked through the camera and saw that the bark had been torn from the tree trunk. I zipped open the blind vent on my left and, as I did so, I glanced at my watch. It was 2:56. I stuck my head out and looked around. The upper 15 feet of the tree was on the ground. Before me was nothing but a ragged, jagged stub—the break was directly through the nest-hole.

Where was the bird? I heard a sound on my left and turned my head to see the female perched on a pine only 12 feet away. As I watched, she pecked slowly at the tree, extended her wings rapidly, fluttered them, closed them, and preened. She continued to extend and flutter her wings every 20 or 30 seconds between periods of slow pecking and preening for the next five minutes, apparently ignoring my exposed head as I moved it this way and that, scanning the vicinity for some sign of the male.

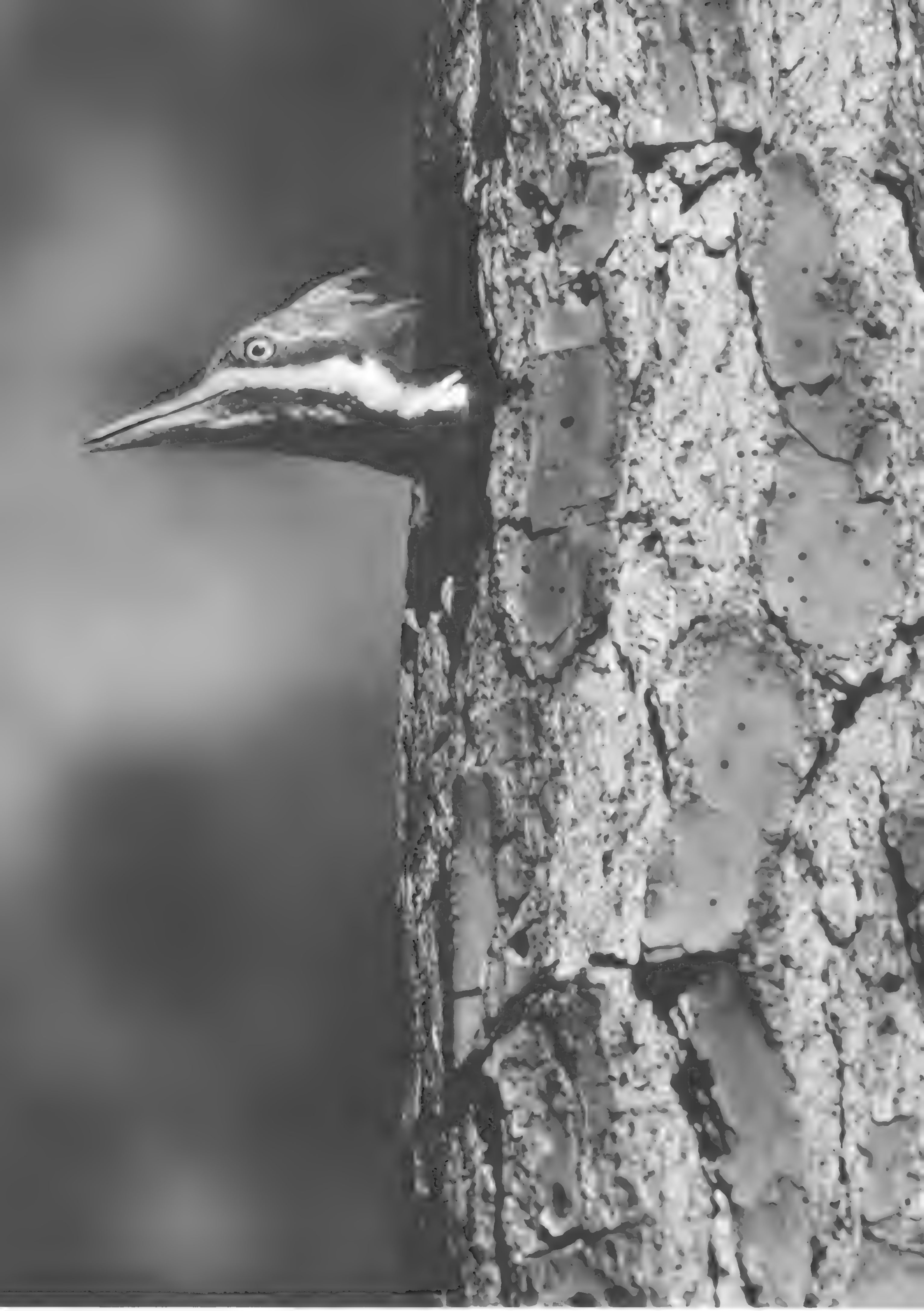
At 3:02 she flew to the broken stub and slowly pecked at the jagged top. Only then did I realize that the nest was exposed and that the bark had been torn from the trunk for about three feet below the broken nest-hole. The female continued to peck very slowly and deliberately; then she backed around the entire barkless area, still pecking slowly as she went. She circled the trunk and stopped just below where the nest-hole had been and of which now only the bottom and about three-quarters of the sides remained. She pecked slowly at the bottom of the nest-hole, looked about her and, finally, down at the ground. She glanced at the prone tree top, flew down to it, and hopped the entire length, still pecking slowly. She hopped from the fallen tree top to the base of the stub and moved upward very slowly—still pecking—to the top where she hesitated and looked down into the nest-cavity. Then she backed into it and disappeared. Almost immediately the upper third of her reappeared. In her bill she carried a slender piece of wood about five inches long, which she dropped over the side to the ground. Again she backed into the cavity and, when her head reappeared, she had an egg crosswise in her bill with the ends protruding from the sides (see Plate I).

Someone should have been there to record my reactions. I snapped the shutter button on the camera but the movement was certainly involuntary. The woodpecker, supporting the egg, which through the lens appeared to be undamaged, against her breast, gradually turned it in her bill until the smaller end pointed forward. Still keeping her body mostly concealed she edged her feet higher in the cavity until the claws hooked over the broken top. Then, after looking about her carefully, she vaulted over the edge into flight and shot past the blind due west and out of my sight.

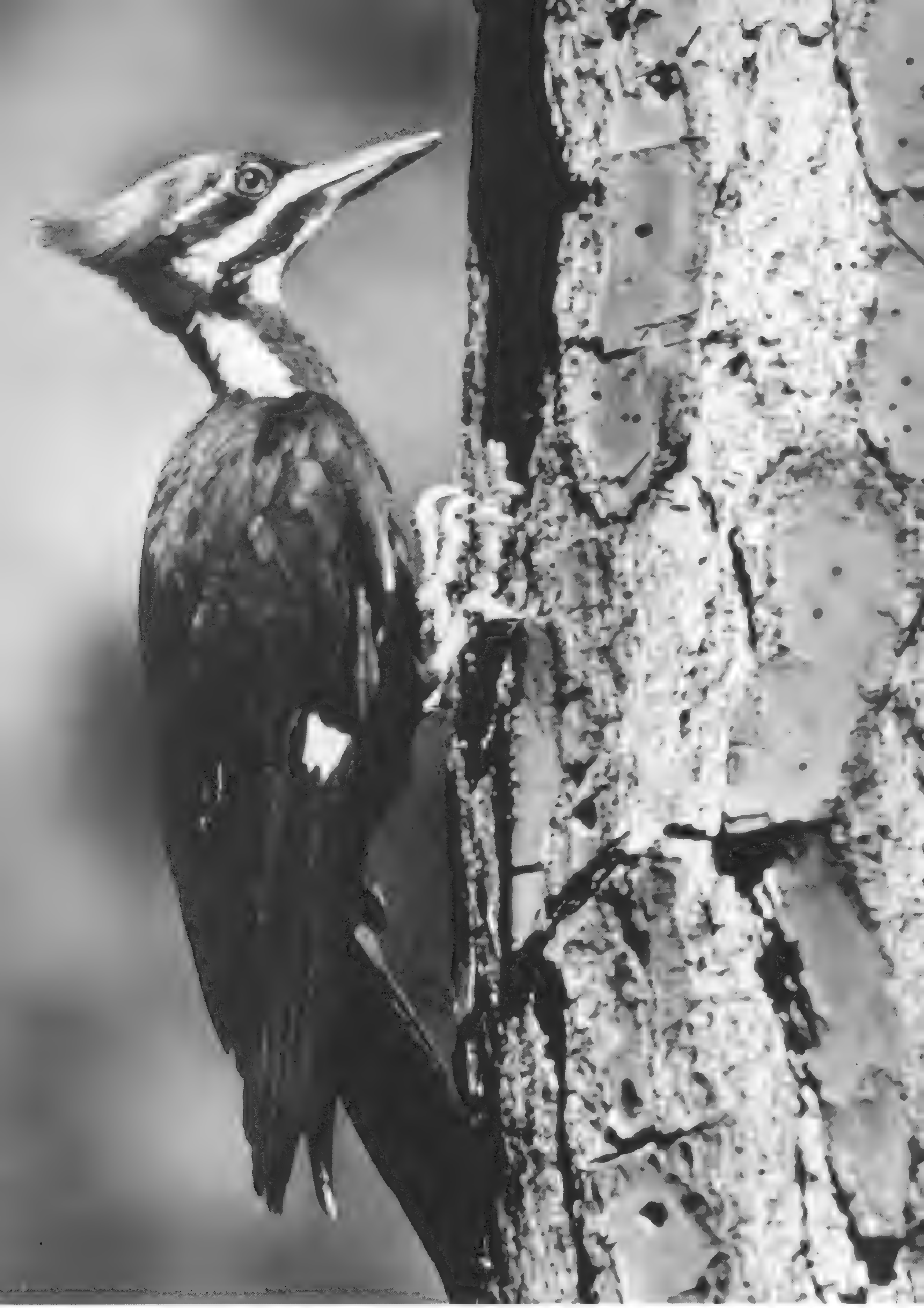
Hastily I zipped open all the vents of the blind so as to be able to see her if and when she returned. I did not have long to wait. In less than two minutes she flew back, landed on top of the stub, and backed down into the cavity. When she reappeared a few seconds later, she had a second egg in her bill, arranged with the small end pointed out. Very quickly she made a vaulting take-off and again flew due west.

This time I was able to watch her flight *clearly* for about 75 yards, as she went low above a woods road to a point where the road turns south, and *partially* for the next 50 yards before she continued west through the pines and out of sight. I am sure that the egg was undamaged and that she did not drop it in the first 75 yards of flight.

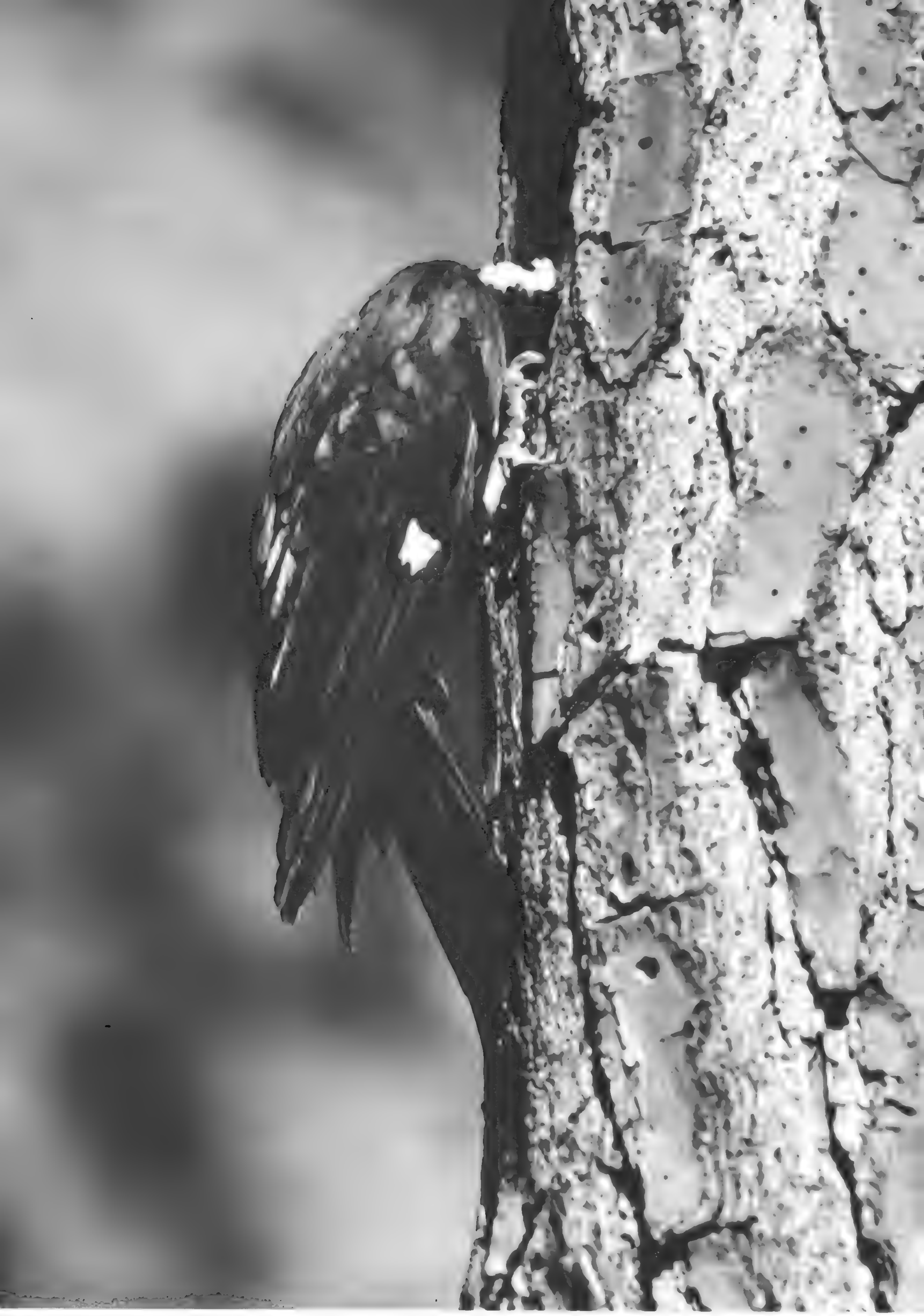
At this point came the nemesis of all photographers—my camera was out of film. Never have tense hands changed a film faster, yet she almost beat me. She was back in less than a minute and a half, had repeated the procedure with the third egg, and was away just as I clicked the take-off shot. I watched



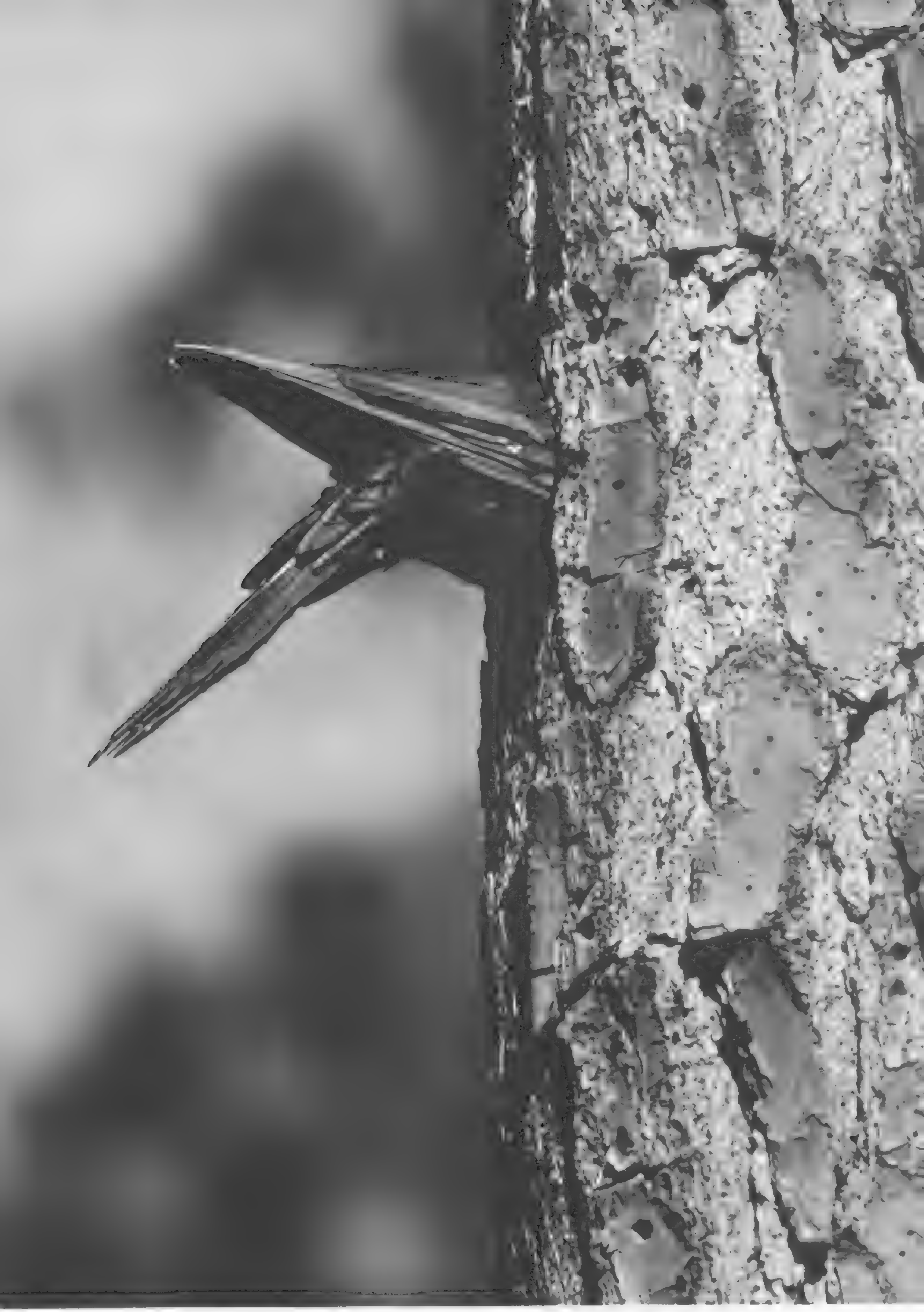
The male Pileated Woodpecker sticks his head out of the nest-hole that he and his mate excavated in an old pine tree near the residential and utility section of Everglades National Park, Florida.



The female Pileated Woodpecker arrives at the nest-hole. Both male and female Pileated Woodpeckers share in the incubation of the eggs. As soon as one bird leaves the other takes over.



The female Pileated Woodpecker starts to enter. Although the length of time between nest changes varies, the average period of time that each bird stayed on the nest during the day was about two hours. At night the male usually does all the incubating.



The female Pileated Woodpecker about to disappear in the nest-cavity. The hole was about 17 feet from the ground in an old tree with a broken top. The diameter of the trunk at the nest-hole was eight and one-half inches.

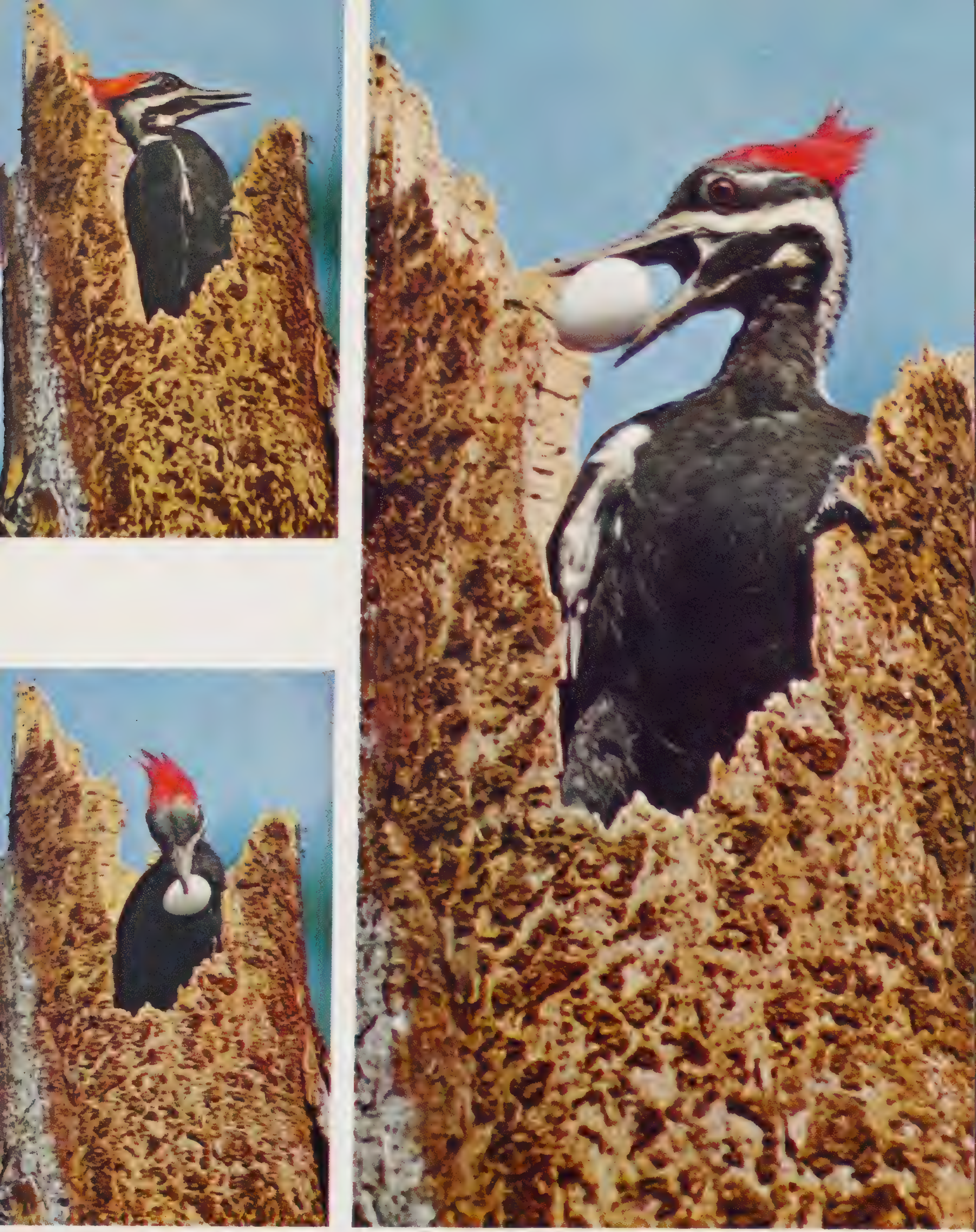


Plate I. After the tree broke off at the nest-hole, the female, which had been incubating the clutch of three eggs at the time, fled to a nearby pine. Six minutes later she returned, examined the jagged edges of the hole, the bark-stripped trunk, and the fallen section of the tree. Then she hopped up the broken stub, backed into the nest-hole and, after first bringing up a slender piece of wood and tossing it to the ground, she backed down into the cavity again (*upper left*) and reappeared with an egg crosswise in her bill (*lower left*). Bracing this first egg against her breast, she slowly turned it until the small end pointed out of her bill (*right*). Gradually she edged up the cavity until her claws clung to the jagged edges. Then she vaulted off (see photograph, next page).

her carry an egg a second time for the first 75 yards and did not see it drop. The time was now 3:12, just 16 minutes since the tree top had crashed.

Five minutes later she returned to the nest-cavity again, proceeding this time much more slowly than before. She perched on the edge and peered into the cavity for several seconds, tapped slowly on the broken top of the stub for several seconds more, looked all about her and down at the ground, and then flew off in the same direction, due west. I did not see her at the nest stub again.

After waiting for one hour and 23 minutes, in hopes that the male would return, I gave up. I descended from the blind at 4:35 and, just as my foot touched the ground, the male flew out of the woods and landed on top of the stub. He had been gone one hour and 45 minutes after the nest change and this was, as far as I know, the first time he had seen the broken tree. Instantly, he was a whirlwind of motion. He hopped around the jagged edge and pecked rapidly at it; he hopped down the trunk just below where the nest-hole had been and drummed; he hopped over the entire area of torn bark. He returned to the top and peered into the cavity. Then he backed into it and disappeared from my sight.

Reappearing in less than a minute, he again pecked rapidly at the jagged edge, but he did not drum. Instead he began calling—a rapid, high-pitched alarm call. He paused for possibly 20 seconds, looked around, and then called again. While he repeated this performance of alternately calling and looking for several minutes, I listened carefully for a reply from the female and heard none.

After about ten minutes on the stub, he flew south across the woods road for some 50 yards and landed on a branch about 45 feet up in a pine tree. I looked through my glasses. The female was there, on the same branch, not three feet from him.

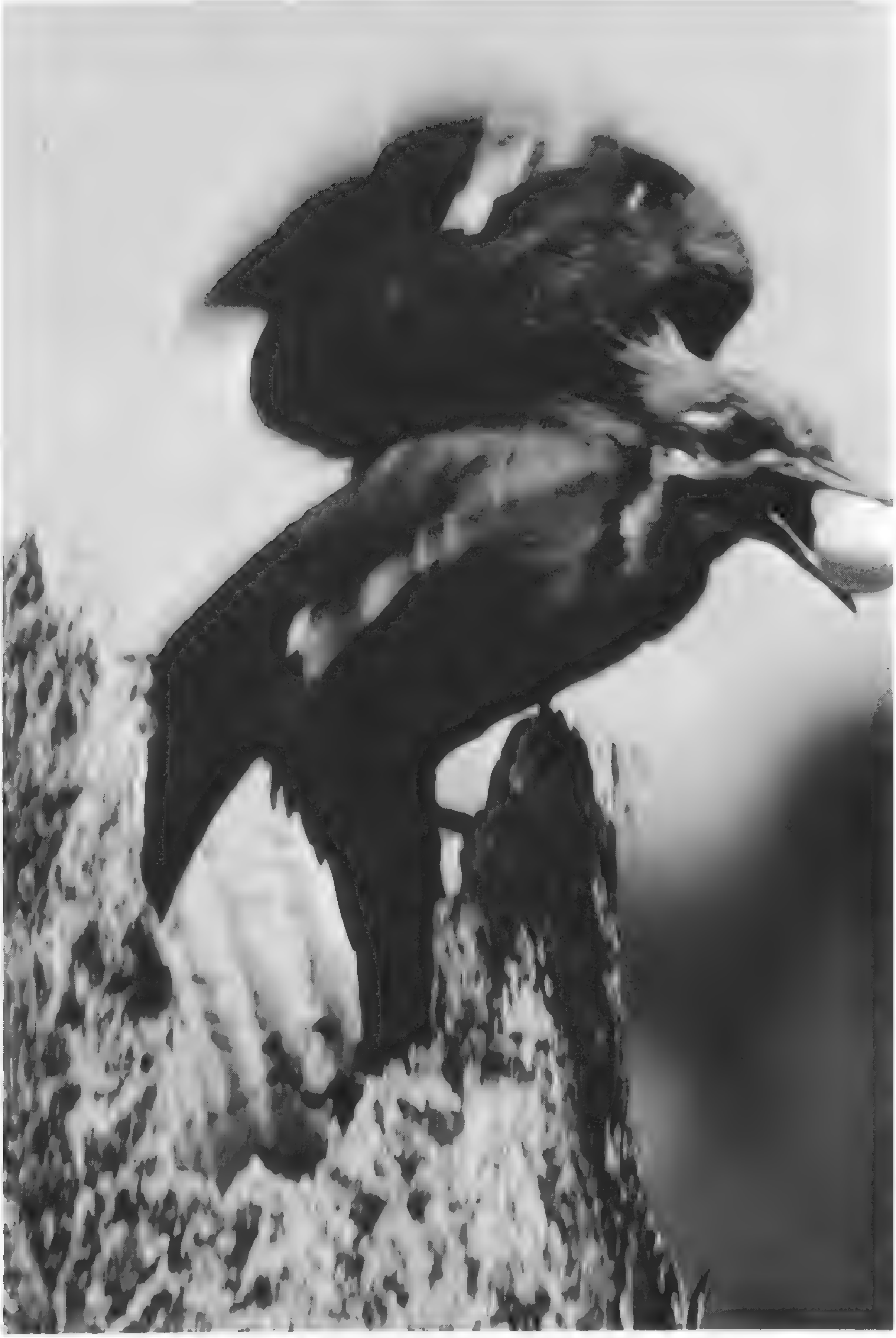
They faced each other. He pecked rapidly at the branch; she pecked slowly. They made no sounds that I could hear and after about three minutes she flew off to the west on approximately the same course she had taken with the eggs and he returned to the pine stub.

Once again he inspected the entire nest-hole area, moving about and pecking more slowly now. He backed down into the cavity several times. He perched on top, looked all around, and then backed down into the cavity again. Finally, he called several times, pausing several seconds between calls. These calls were the multi-note ones, loud, but not with the rapid sequence of the alarm calls he had uttered previously. I heard no answer from the female. After about 15 minutes on the stub, he flew off to the south and vanished into the pine woods. It was now 4:55 PM, just 20 minutes since his first arrival at the damaged nest. I never saw him near the nest stub again.

All during that 20 minutes he had paid no attention to me standing on the ground within 12 or 15 feet of the stub and making no attempt to move quietly. The shyness that both birds had shown since the beginning of incubation seemed to have gone.

Ranger Carlson returned at 4:45 to find me standing in the woods road, staring at the male on the broken stub. I suppose my mouth was still open. I do know I was glad of this eye-witness.

At 5:00 PM, we climbed the tree stub to inspect the cavity in which nothing remained except a few chips and some dry dusty material. The female had removed the entire clutch of three eggs. As I examined the stub, which was about 8.5 inches in diameter at the nest level, I was not surprised



The female Pileated Woodpecker, carrying the third egg in her bill, vaults from her broken-open nest in a swift, straight flight and disappears in a pine woods.

that the tree had collapsed. The birds had hollowed it out so completely that the walls were only a fragile shell from one-quarter to one-half inch thick.

The rest is anticlimax. At the suggestion of Heinz Sielmann, an authority on woodpeckers who was visiting me at the time, I returned to the area of the damaged nest several hours on each of the next five days.

On 17 April, Dr. and Mrs. Frederick T. Ranson spent three and one-half hours searching. They spotted the male and followed him as he moved about continuously, climbing trees, inspecting old holes, hopping, and pecking, but they did not see the female.

On 18 April, I searched the woods for three hours. I saw the male "check" eight different nest-holes. He stayed from five to 20 minutes at each, examining and pecking around the tree for a distance of several feet above and below the hole. Again, there was no sign of the female.

On 19 April, I found both birds and watched them for four hours while they climbed trees and checked holes. They stayed close together, within a few feet or at most a few yards of each other all the time.

On 20 and 21 April, Ranger Carlson and I watched the Pileated Woodpeckers working on a new hole in the utility pole in front of the fire headquarters building, the same pole they had excavated previously. The new hole was about three feet below the old one on the same side. While the birds worked, Mr. Carlson made a real effort to keep everyone away from the area, even to the point of having the personnel use the back door of the building. But his efforts were in vain. After working for two days, the woodpeckers gave up this hole and moved on. I ceased to look for them.

In my search for the birds and the eggs I had but one clue. I knew of a hole where the female often roosted when she was not incubating. It was about 150 yards west of the nesting stub. This story would have a perfect ending if I had found the eggs there. Unfortunately, I did not. When I tapped on the tree where the eggs should have been, a very irate Yellow-shafted Flicker (*Colaptes auratus*) stuck its head out.

The first reactions of several ornithologists to this report were disbelief. And their comments after seeing the pictures ranged from "I have never heard of any behavior of a comparable type" (William Beckwith Robertson, Jr.), "a real ornithological scoop" (Sally Hoyt Spofford), and "a real thriller" (Olin Sewall Pettingill, Jr.) to "I've never heard of such behavior" (Alexander Wetmore) and "to me unique" (Roger Tory Peterson).

I have since learned of one other instance of a woodpecker—a Yellow-shafted Flicker—carrying an egg. I add only a brief summary of a letter:

George P. Hitchcock, attracted by a racket on the edge of a grove of scrub pines near Orleans, Massachusetts, found a Starling (*Sturnus vulgaris*) and a flicker quarreling close to the flicker's nest-hole. Mr. Hitchcock hurried for his camera and, while he was setting it up and adjusting the focus, the Starling disappeared and the flicker flew in and out of the hole and back and forth into the woods several times. Then it entered the cavity and popped its head out and looked around. By the time the bird repeated this procedure three times, the photographer was ready. He decided: "The next time the head comes out I'll shoot."

The next time the whole bird popped out, flew straight over the camera-man and his wife and disappeared into the grove. Mrs. Hitchcock was positive the bird was carrying something; Mr. Hitchcock was too busy with the camera to be sure. They had to wait for the film to be developed before they knew. And in the finished picture, which he kindly sent me, was clear proof—the flicker was carrying an egg crosswise in its bill.

I am sure that something like my experience with the Pileated Woodpecker can only happen once in a life time, but I know that the episode will act as a prod to keep me going. And when I am hot and tired and thirsty and aching to leave the blind, I will straighten up, put more film in the camera, and wonder just what the bird is going to do next.

1410 NORTHWEST SECOND AVENUE, HOMESTEAD, FLORIDA

COVER PAINTING OF THE GREEN ARACARI

ARTHUR SINGER

I had my first view of the Green Aracari (*Pteroglossus viridis*) about two years ago in Surinam. Don and Virginia Eckelberry and I were driving slowly from Paramaribo to Moengo along one of that country's few roads when Virginia spotted four of these brilliantly colored birds sitting in a cecropia tree quite close to the road. Fortunately, like many tropical birds, they were extremely lethargic and after my first startled gasp of surprise I had plenty of time to take color photographs of them before they moved on. I really did not need the photographs, for the visual image of those four handsome birds in the lush tropical vegetation stayed with me. I resolved then to paint just such a picture some day. The cover of this issue of *The Living Bird* gave me the opportunity—or was it the excuse?

The Green Aracari—pronounced *ar-a-sary*—occurs in eastern Venezuela, the Guianas, and Brazil, north of the Amazon and east of the Rio Negro and is not particularly rare. Although Count Buffon, the 18th century naturalist, may have included it in his work, Barraband and Gould are the only other artists I know of who have painted this species. I rendered it previously in "Birds of the World" by Oliver L. Austin, Jr. (1962), having seen the bird alive when one was exhibited by the New York Zoological Society sometime between 1939 and 1943.

The Green Aracari is but one of 37 clownish-looking toucans (family Ramphastidae) found from Mexico to southern Brazil, Paraguay, and Argentina. They are all rather large, varying in length from one to two feet. Much of the length is in their large and very colorful bills — the toucans' most distinctive feature. This gives toucans a top-heavy appearance. Actually the bill is very light, its internal structure consisting only of a spongy network of thread-like strands of bone, and it has several functions: it is a "long arm" that adroitly plucks fruit from trees; it undoubtedly becomes a formidable weapon of defense when necessary; and it probably serves as a display in courtship and a factor in species recognition.

Although toucans subsist mostly on fruit, they also consume insects and prey upon amphibians, small reptiles, and the eggs and nestlings of other birds.

When they are not breeding, toucans commonly move about in the vegetation in small flocks. However, one rarely sees them flying together; more often they fly singly from tree to tree. Even though they live in the tropics and subtropics and are therefore quite sedentary, some of the higher Andean forms wander to lower altitudes in certain months. Their voices are unmusical croakings, barks, rattles, bugles, and bill-clackings — all for the most part unpleasant to the ear.

As do most other members of their order (Piciformes), toucans nest in holes in trees—natural cavities or, more frequently, abandoned woodpecker holes that may have been enlarged—and lay from one to four glossy white eggs. An unusually flexible articulation of the tail vertebrae permits the toucan to fold its tail against its back when it is moving about within its relatively small nest-cavity.

Both the male and female incubate the eggs during the short incubation period—16 days in the Blue-throated Toucanet (*Aulacorhynchus caeruleogularis*). And both feed the young, blind and naked when hatched, during the nestling period which is frequently quite long—six to seven weeks in the Keel-billed Toucan (*Ramphastos sulfuratus*).

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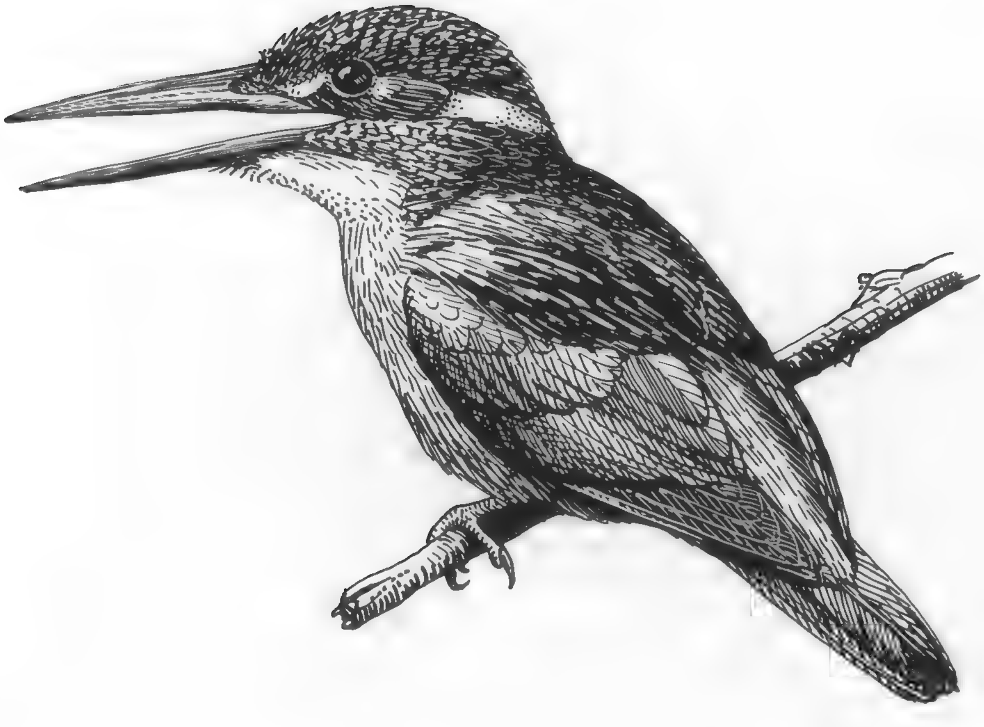
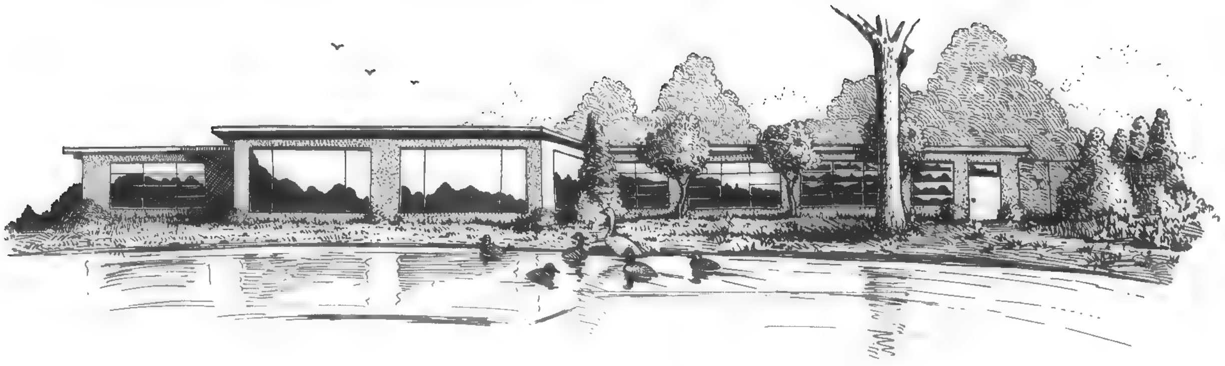


Common Kingfisher, *Alcedo atthis*



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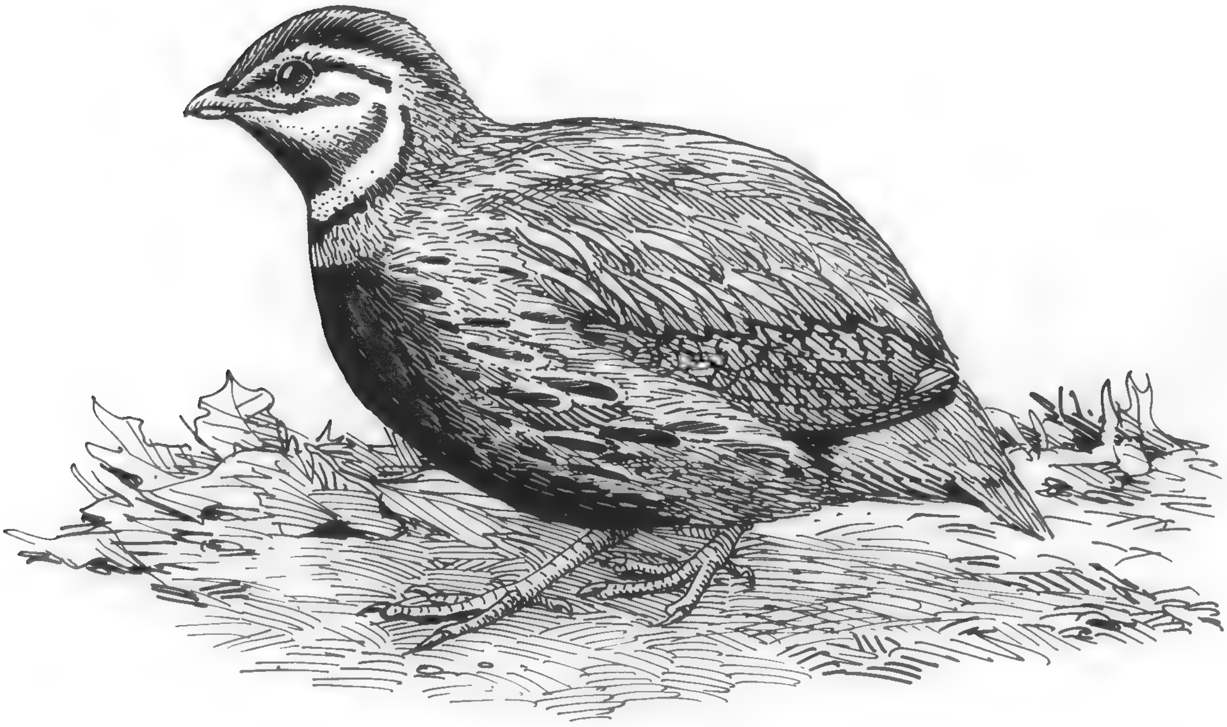

Black-breasted Quail, *Coturnix coromandelica*

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Kaj Ejvind Westerskov
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Mrs. O. L. Westgate
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Laidlaw Williams
Mrs. Ruth Williams
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Irving Wolf
Mark A. Wolf
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A. H. Wright
Walter Wust

Y. Yamashina
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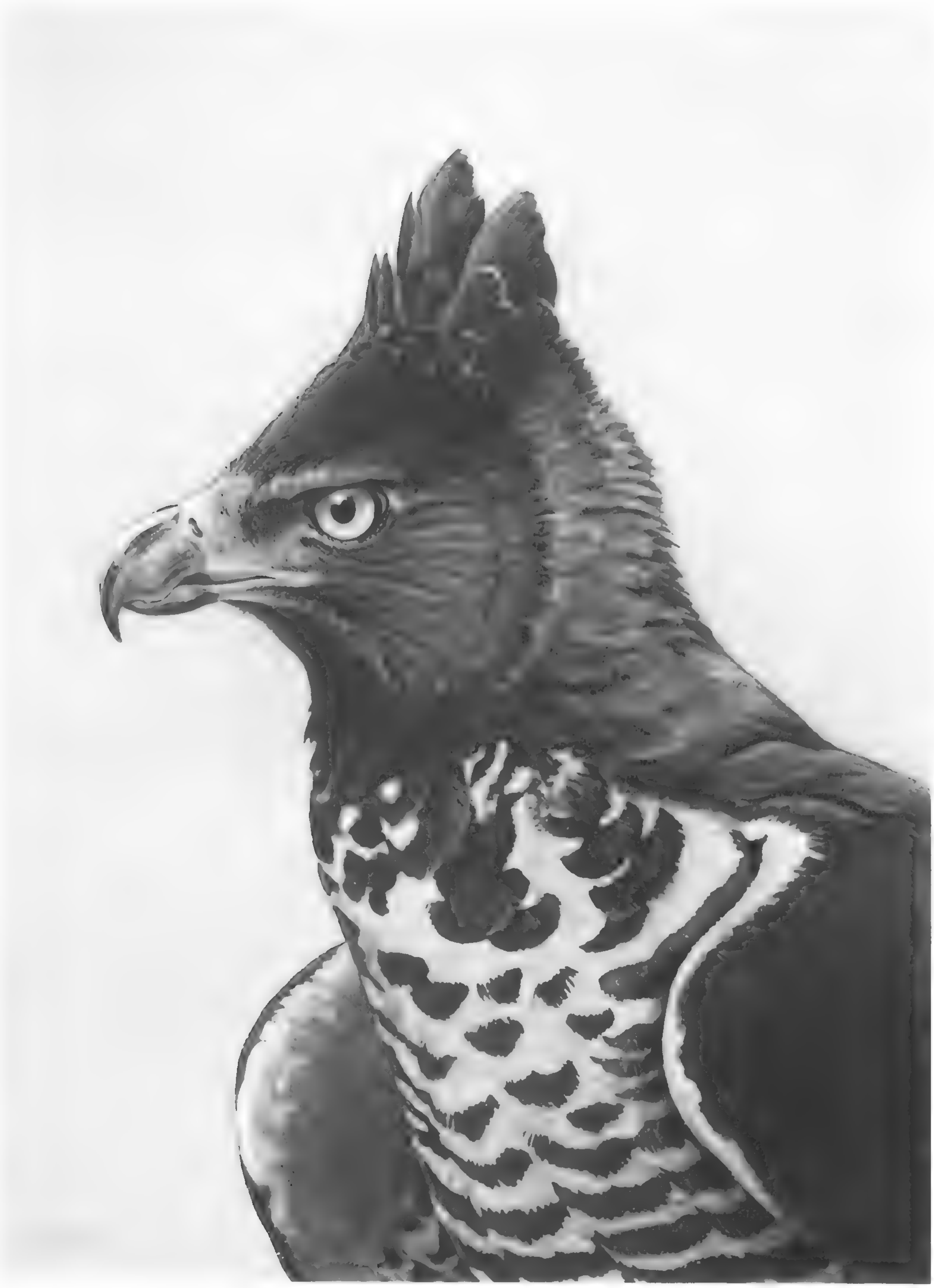
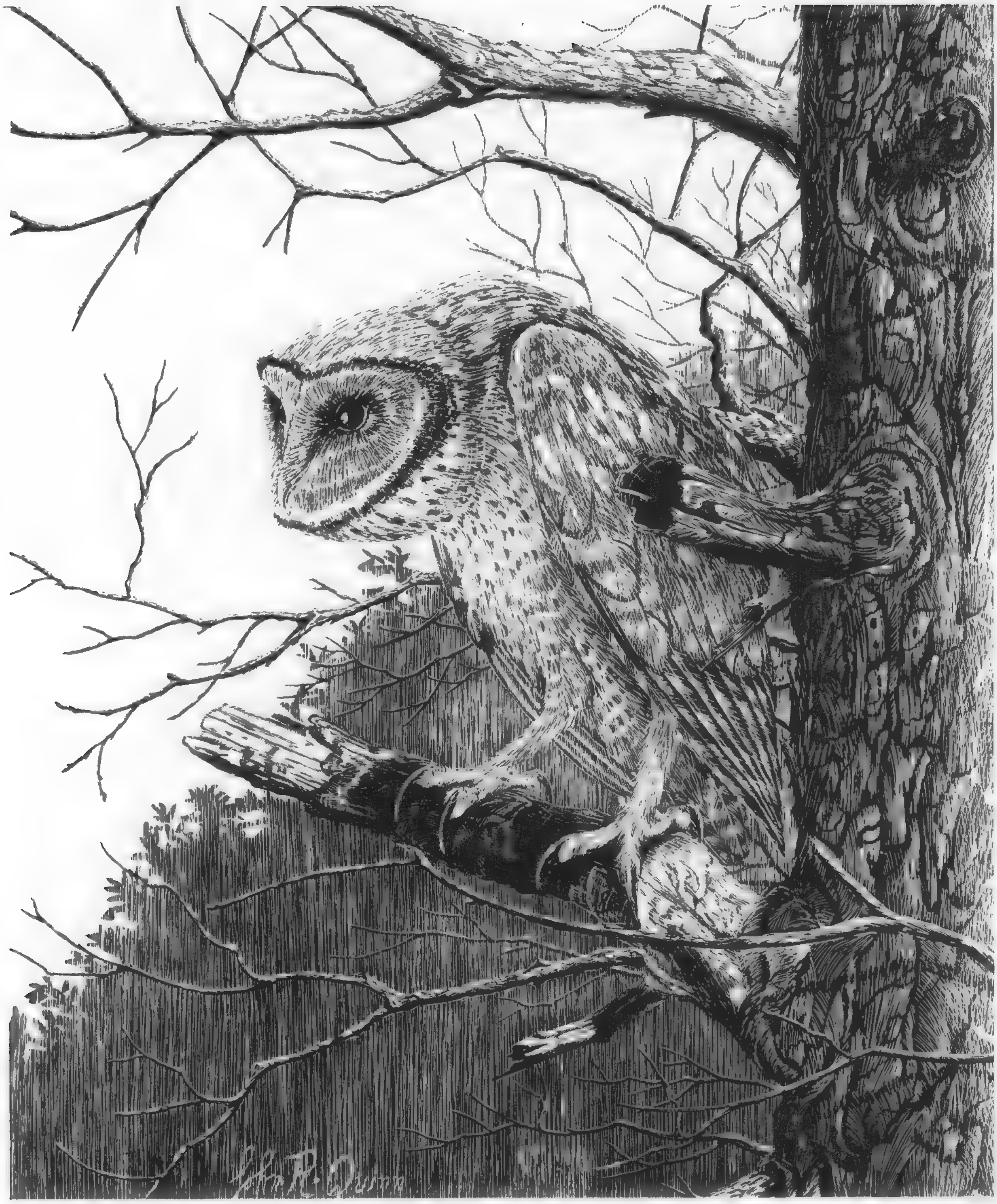
Dale A. Zimmerman
Richard L. Zusi
J. L. Zwingle
Mrs. J. L. Zwingle



Crowned Eagle, *Stephanoaëtus coronatus.* Painting by Al Gilbert.


John R. Quinn

Masked Owl, *Tyto novaehollandiae*. Drawing by John R. Quinn.

THE LIVING BIRD

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An important part of the Laboratory's educational work is the production of motion-picture films and phonograph records of birds with matching color slides for use in schools and adult organizations.

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